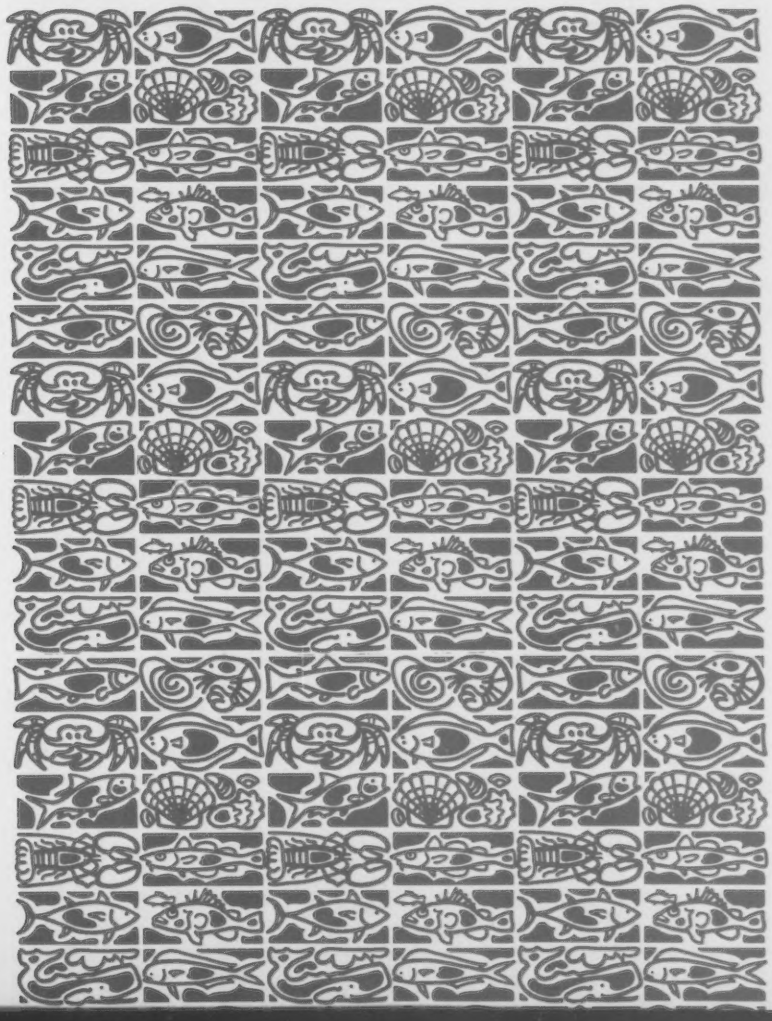
U.S. Department
of Commerce

Volume 89
Number 1
January 1991

Fishery Bulletin



U.S. Department of Commerce
Robert Mosbacher
Secretary

National Oceanic and Atmospheric Administration
John A. Knauss
Under Secretary for
Oceans and Atmosphere

National Marine Fisheries Service
William W. Fox, Jr.
Assistant Administrator
for Fisheries

Fishery Bulletin

Scientific Editor
Dr. Linda L. Jones
National Marine Mammal Laboratory
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE
Seattle, Washington 98115-0070

Editorial Committee
Dr. Andrew E. Dizon National Marine Fisheries Service
Dr. Charles W. Fowler National Marine Fisheries Service
Dr. Richard D. Methot National Marine Fisheries Service
Dr. Theodore W. Pietsch University of Washington
Dr. Tim D. Smith National Marine Fisheries Service
Dr. Mia J. Tegner Scripps Institution of Oceanography

Managing Editor
Nancy Peacock
National Marine Fisheries Service
Scientific Publications Office
7600 Sand Point Way NE, BIN C15700
Seattle, Washington 98115-0070

The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Second class postage is paid in Seattle, Wash., and additional offices. POSTMASTER send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402.

Although the contents have not been copyrighted and may be reprinted entirely, reference to source is appreciated.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $16.00 domestic and $20.00 foreign. Cost per single issue: $9.00 domestic and $11.25 foreign.

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

U.S. Department
of Commerce
Seattle, Washington

Volume 89
Number 1
January 1991

Fishery Bulletin

Contents

1 **Beckman, Daniel W., A. Louise Stanley, Jeffrey H. Render, and Charles A. Wilson**
Age and growth-rate estimation of sheepshead *Archosargus probatocephalus* in Louisiana waters using otoliths

9 **DeMartini, Edward E.**
Annual variations in fecundity, egg size, and the gonadal and somatic conditions of queenfish *Seriphus politus* (Sciaenidae)

19 **Ferreira, Beatrice Padovani, and Carolus Maria Vooren**
Age, growth, and structure of vertebra in the school shark *Galeorhinus galeus* (Linnaeus, 1758) from southern Brazil

33 **Grant, George C.**
Chaetognatha from the central and southern Middle Atlantic Bight: Species composition, temperature-salinity relationships, and interspecific associations

41 **Hannah, Robert W., and Stephen A. Jones**
Fishery-induced changes in the population structure of pink shrimp *Pandalus jordani*

53 **Kimura, Daniel K., and Julaine J. Lyons**
Between-reader bias and variability in the age-determination process

61 **Lavalli, Kari L.**
Survival and growth of early-juvenile American lobsters *Homarus americanus* through their first season while fed diets of mesoplankton, microplankton, and frozen brine shrimp

69 **Ledgerwood, Richard D., Frank P. Thrower, and Earl M. Dawley**
Diel sampling of migratory juvenile salmonids in the Columbia River Estuary

79 **Lozano-Alvarez, Enrique, Patricia Briones-Fourzan, and Bruce F. Phillips**
Fishery characteristics, growth, and movements of the spiny lobster *Panulirus argus* in Bahia de la Ascension, Mexico

91 **Matlock, Gary C., Walter R. Nelson, Robert S. Jones, Albert W. Green, Terry J. Cody, Elmer Gutherz, and Jeff Doerzbacher**
Comparison of two techniques for estimating tilefish, yellowedge grouper, and other deepwater fish populations

101 **Murphy, Michael D., and Mark E. Chittenden Jr.**
Reproduction, age and growth, and movements of the gulf butterfish *Peprilus burti*

117 **Overholtz, William J., Steven A. Murawski, and William L. Michaels**
Impact of compensatory responses on assessment advice for the northwest Atlantic mackerel stock

129 **Polovina, Jeffrey J.**
Evaluation of hatchery releases of juveniles to enhance rockfish stocks, with application to Pacific Ocean perch *Sebastes alutus*

137 **Smith, Barry D., and Glen S. Jamieson**
Movement, spatial distribution, and mortality of male and female Dungeness crab *Cancer magister* near Tofino, British Columbia

149 **Stanley, David R., and Charles A. Wilson**
Factors affecting the abundance of selected fishes near oil and gas platforms in the northern Gulf of Mexico

161 **Temte, Jonathan L.**
Use of serum progesterone and testosterone to estimate sexual maturity in Dall's porpoise *Phocoenoides dalli*

Note

167 **Somerton, David A.**
Detecting differences in fish diets

Actual publication dates of issues in *Fishery Bulletin* volumes 87 and 88:

87(1) July 1989	88(1) June 1990
87(2) September 1989	88(2) August 1990
87(3) April 1990	88(3) October 1990
87(4) August 1990	88(4) December 1990

Abstract.– Ages were estimated for sheepshead *Archosargus probatocephalus* (Pisces:Sparidae) from Louisiana waters using transverse sections of sagittae (otoliths). Opaque annuli were validated to have formed in sagittae once per year during April and May in 1987 and 1988. Age range was 1–20 years for fish measuring 22–56 cm fork length and weighing 0.4–3.6 kg. Von Bertalanffy growth models were different for males and females; females exhibited a faster growth rate and achieved larger maximum sizes. There was great variability in age at a given length or weight, which precludes the use of morphometrics as age indices. Otolith weight provided a more precise estimate of age than fish length or weight. The consideration of fish length or weight in addition to otolith weight significantly improved the predictive capability of multiple regression models.

Manuscript accepted 8 August 1990.
Fishery Bulletin, U.S. 89:1–8 (1991).

Age and Growth-Rate Estimation of Sheepshead *Archosargus probatocephalus* in Louisiana Waters Using Otoliths

Daniel W. Beckman
A. Louise Stanley
Jeffrey H. Render
Charles A. Wilson

Coastal Fisheries Institute, Center for Wetland Resources
Louisiana State University, Baton Rouge, Louisiana 70803-7503

The sheepshead *Archosargus probatocephalus* is an estuarine/marine sparid common in coastal waters of the northern Gulf of Mexico. This species supports significant commercial and recreational fisheries off Louisiana. Louisiana commercial landings of sheepshead have increased substantially in recent years, from 59 to 1111 metric tons between 1981 and 1989 (NMFS 1982, 1990), resulting in concern for the species and consideration of development of a management plan. However, little has been reported on sheepshead biology and population dynamics. Of particular concern is the lack of information on age and growth. The only information reported are average growth rates for juveniles in North Carolina (Hildebrand and Cable 1938) and Florida (Springer and Woodburn 1960). The development of valid management plans based on the current available information would be difficult.

Otolith analyses have been proven valid for age estimation of several fish species occurring in the temperate waters of the northern Gulf of Mexico (Johnson et al. 1983, Barger 1985, Beckman et al. 1989, Beckman et al. 1990a). Sectioning of otoliths is often required in order to accurately enumerate annuli for age estimation, especially for long-lived species with large robust otoliths. Sample preparation and ageing are often labor intensive. As an alternative, Boehlert (1985) suggested that otolith size may provide objective, repeatable age estimates and save time and cost in sample processing. Several studies have documented otolith size as greater for older fish than for younger fish of the same size (Templeman and Squires 1956, Wilson and Dean 1983, Boehlert 1985, Reznick et al. 1989, Secor and Dean 1989), and suggested that otolith weight be used to estimate age.

The purposes of this study were to validate age estimates of sheepshead in Louisiana waters using otolith (sagitta) transverse sections, to derive fish growth models, and to determine the potential of using otolith weight for age estimation of this species.

Methods

We sampled sheepshead ($n = 784$) from February 1987 to August 1988. Samples were taken by commercial gillnet (15–18 cm [6–7 inch] stretch mesh) ($n = 461$), trawl ($n = 163$), and haul seine ($n = 43$); recreational hook-and-line ($n = 38$) and spearfishing ($n = 27$); and unknown gear types ($n = 52$). Gillnet and haul seine samples were predominantly from inshore waters in the Mississippi Delta–Lake

Pontchartrain region. Trawl samples were from waters offshore of the Mississippi Delta region. Hook-and-line and spearfish samples were predominantly captured around offshore oil and gas structures during fishing tournaments.

Fork length (FL, mm), total weight (W, g), and sex were recorded and sagittae (otoliths) were removed, stored dry, and weighed (unless damaged in removal). Otoliths were prepared and examined for age determination as described by Beckman et al. (1989). Sagittae were embedded in an epoxy resin medium (Spurr 1969), sectioned in the transverse plane using a Buehler Isomet low-speed saw, mounted on glass slides, and viewed at 15–40× using a stereomicroscope. Terminology is used as defined by Wilson et al. (1987).

Three readers independently counted annuli in each otolith section and estimated the degree of completion of the marginal annulus, as follows: When any portion of an annulus was present at the growing edge, the margin was referred to as "opaque." Translucent edges were assigned to one of three categories: + indicated a translucent zone judged to be 0 to 1/3 complete; ++, 1/3 to 2/3 complete; and +++, 2/3 to totally complete. The completeness of translucent zones was judged based on the estimated width of the adjacent translucent zone and the widths of comparable zones in other otoliths.

We assigned ages based on annulus counts, assuming a 1 January date of birth for convenience and based on spawning periodicity (Wilson et al. 1988).

We validated age estimates by marginal increment analysis, which documents the time of annulus formation at the otolith's edge. Reproducibility of age estimates was determined using the coefficient of variation, index of precision (Chang 1982), and average percent error (Beamish and Fournier 1981). The ages used in analyses were those upon which at least two of the readers agreed. If all readers disagreed on age estimates, the fish was excluded from analyses.

Fork length–weight regressions were fit to the data using the model: $\text{Weight} = aFL^b$. Regressions for males and females were compared using analysis of covariance (Ott 1988).

Growth curves were fit by nonlinear regression on raw data (Statistical Analysis Systems 1985). The growth equation for length (von Bertalanffy 1938, 1957) was of the form: $L_t = L_\infty[1 - e^{-K(t-t_0)}]$, and for weight $W_t = W_\infty[1 - e^{-K(t-t_0)}]^b$, where L_t and W_t are the estimated length and weight, L_∞ and W_∞ are the asymptotic length and weight, K is the growth coefficient, t is the age (years), t_0 is the hypothetical age when length or weight would be zero, and b is the exponent from the length-weight regression.

Plots of residuals from regression models were used to check the assumption of normality (Sokal and Rohlf 1981). To test for differences in growth for males and females, a full model, in which sexes were modeled separately, was compared with a reduced model, in which sexes were grouped. An F-test (Ott 1988) was used to test for differences in the models.

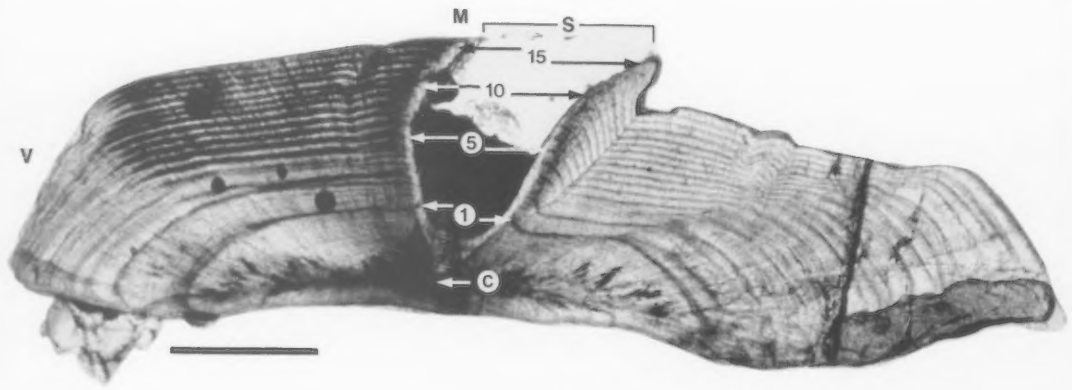


Figure 1

Photomicrograph of a transverse section of a sheepshead otolith (sagitta) under transmitted light. Numbers identify annuli. There are 15 annuli, the margin is translucent, and the fish was captured in February 1988. C = core; S = sulcus; M = medial; V = ventral; Bar = 1 mm.

Multiple linear-regression models were used to estimate age based on otolith weight and fish size. Regressions were fit in a stepwise manner (Statistical Analysis Systems 1985). Independent variables included in models were otolith weight (OW), fork length (FL), total weight (W), condition factor ($CF = W/FL^b$), square and cubic terms for length and weight, and interaction terms (OW–FL, OW–W, OW–CF). All variables were log-transformed to meet the assumptions of normality and homogeneous variances. Regressions for males and females were compared using analysis of covariance.

Results and discussion

In sheepshead, the sagitta is the largest otolith and is oval-shaped with a pointed rostrum. It is laterally compressed with a deeply indented sulcus on its medial surface. It was not possible to discern all annuli for age estimation in whole sagittae. Thin transverse sections exposed narrow opaque and broad translucent zones which alternated from the core out to the growing edge (Fig. 1). Although it was not the axis of most rapid growth, the only axis where annuli were consistently deposited was on the medial surface, ventral to the sulcus (Fig. 1). Counts of annuli (opaque zones) and marginal increment analyses were made in this region using transmitted light. Annulus deposition was either inconsistent or discontinuous in other regions of the sagittae, since annuli were indiscernible there.

One annulus formed per year on the medial surface of sheepshead sagittae. Annulus formation occurred primarily during April and May in 1987 and 1988 (Fig. 2). A translucent zone was formed continuously during non-annulus-forming months, as indicated by the progression of peaks for each marginal index. A substantial translucent zone had formed in most otoliths by July and was estimated as greater than 2/3 complete by December, although most otoliths did not begin annulus formation until the following April.

Only three otoliths (0.4%) were excluded from analyses due to lack of agreement on age estimates among the three readers. At least two readers agreed on ages for all other fish, and these age estimates were used in analyses. All three readers agreed on 75% (566 of 758) of age estimates. Ageing precision was high, based on a mean coefficient of variation (V) of 0.0304, a mean index of precision (D) of 0.0175, and an average percent error (APE) of 0.0234.

Annulus deposition in sheepshead otoliths coincided with its reported peak spawning period (March–April; Wilson et al. 1988). However, annulus formation is apparently not a direct result of spawning since it occurred during the same period in mature and immature fish. Reported age at first reproduction is 2–4 years (Wilson et al. 1988). Annuli were deposited in sheepshead otoliths over a similar, but shorter, time period (April–May) as reported for red drum *Sciaenops ocellatus* (January–May; Beckman et al. 1989), black

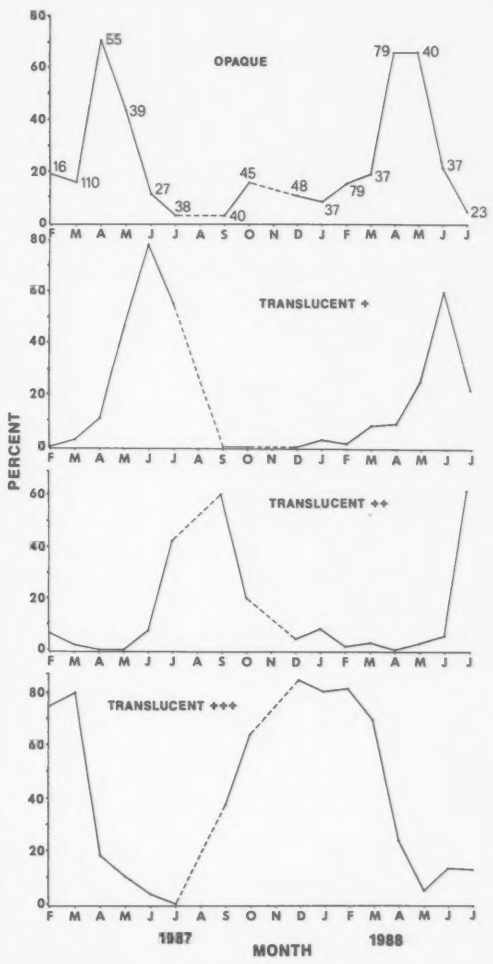


Figure 2

Plot of percent frequency of margin conditions in otoliths (sagittae) of sheepshead vs. month of capture. "Opaque" margins refer to an annulus at the growing edge. "Translucent" margin conditions indicate the estimated degree of completion of the translucent zone at the growing edge: (+) 0 to 1/3 complete; (++) 1/3 to 2/3 complete; (+++) 2/3 to totally complete. Numbers next to the points for opaque margins indicate the sample size for each month.

Table 1

Summary of age and growth analyses of sparids. K and L_∞ are parameters from von Bertalanffy growth models. Age and length are the maximums reported by the source. Lengths marked (*) are total lengths, others are fork lengths. M and F refer to parameters for males and females, when reported.

Species	Source	Location		K	L_∞	Age (max.)	Length (max.)
Archosargus probatocephalus	This study	N. Gulf of Mexico	(M)	0.42	419	20	500
			(F)	0.37	446	20	500
Stenotomus caprinus	Geoghegan and Chittenden (1982)	N. Gulf of Mexico		—	—	3	193
Calamus leucosteus	Waltz et al. (1982)	U.S. Atlantic		0.17	331	12	410
Pagrus pagrus	Manooch and Huntsman (1977)	U.S. Atlantic		0.10	763	15	*690
Stenotomus chrysops	Finkelstein (1969)	U.S. Atlantic	(M)	0.27	343	15	370
			(F)	0.23	374		
Cheimerius nufar	Coetzee and Baird (1981)	South Africa		0.07	954	22	*705
Cymatoceps nasutus	Buxton and Clarke (1989)	South Africa		0.05	1090	45	1099
Pachymetopon aeneum	Buxton and Clarke (1986)	South Africa		0.13	467	12	400
Pachymetopon blochii	Pulfrich and Griffiths (1988)	South Africa		0.16	411	12	350
Pterogymnus laniarius	Hecht and Baird (1977)	South Africa		0.19	481	11	*422
Pagellus bellottii	Koranteng and Pitcher (1987)	Ghana	(M)	0.38	257	6	250
			(F)	0.23	286		
Pagrus major	Sakamoto (1984)	Japan		0.21	670	10	590
Chrysophrys auratus	Horn (1986)	New Zealand		—	—	60	650

drum *Pogonias cromis* (January–April; Beckman et al. 1990a), and Atlantic croaker *Micropogonias undulatus* (February–April; Barger 1985) in the northern Gulf of Mexico. It is likely that annulus formation in sagittae of these species is in response to environmental factors and is not related to reproductive seasonality, since all three species exhibit different spawning seasons: red drum, August–October (Wilson et al. 1989); black drum, December–April (Beckman et al. 1990b); Atlantic croaker, September–March (White and Chittenden 1987).

Sheepshead are relatively long-lived, with a maximum life span of at least 20 years based on our estimates. Greater ages are likely since the Louisiana gamefish record is 9.6 kg (Louisiana Outdoor Writers Assoc. 1987), and the maximum sized fish in this study was 3.9 kg. The maximum age we observed for sheepshead is greater than reported for other Gulf/U.S. Atlantic sparids (Table 1). However, great longevity is apparently not unusual for this family, as greater maximum ages have been reported for sparids elsewhere (Table 1).

Length–weight regressions for males and females were not significantly different ($P = 0.991$ for intercepts, $P = 0.647$ for slopes). However, since the exponents are used in growth models, regressions are presented for both sexes. Regressions were,

for males:

$$\text{Weight} = 4.48 \times 10^{-5}\ \text{FL}^{2.88} \quad r^2 = 0.943$$

for females:

$$\text{Weight} = 5.30 \times 10^{-5}\ \text{FL}^{2.85} \quad r^2 = 0.926$$

sexes combined:

$$\text{Weight} = 5.46 \times 10^{-5}\ \text{FL}^{2.86} \quad r^2 = 0.923.$$

The separation of sexes in growth models resulted in a significantly better fit by length and weight when compared with models in which sexes were combined ($P<0.001$). Therefore, separate von Bertalanffy growth curves for males and females were used to model growth in length (Fig. 3) and weight (Fig. 4). Residuals appeared normally distributed about the regression lines. Growth models fit were, by length,

males:

$$L_t = 419(1 - e^{-0.417(t+0.901)}) \quad r^2 = 0.589$$

females:

$$L_t = 447(1 - e^{-0.367(t+1.025)}) \quad r^2 = 0.532,$$

and by weight,

males:

$$W_t = 1900(1 - e^{-0.280(t+2.657)})^{2.88} \quad r^2 = 0.549$$

females:

$$W_t = 2557(1 - e^{-0.219(t+3.061)})^{2.85} \quad r^2 = 0.474,$$

The growth curves suggest rapid growth for sheepshead to an age of 6–8 years, after which an asymptote is approached. The values of K, the von Bertalanffy growth coefficient, for sheepshead are relatively high when compared with other sparids (Table 1) and to nonsparid perciform fish of similar size (see Pauly 1980). This indicates that sheepshead exhibit relatively rapid growth to an asymptotic size. This could be a result of living in the highly productive waters adjacent to the Mississippi Delta.

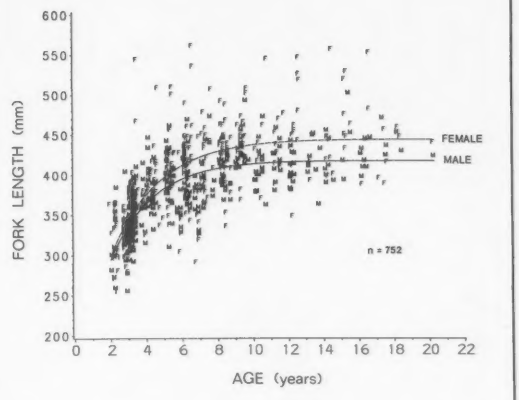


Figure 3
Von Bertalanffy growth models by length for male and female sheepshead. M = male; F = female.

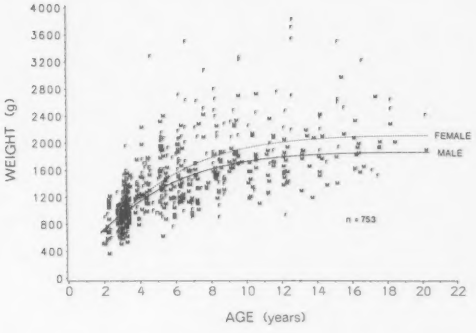


Figure 4
Von Bertalanffy growth models by weight for male and female sheepshead. M = male; F = female.

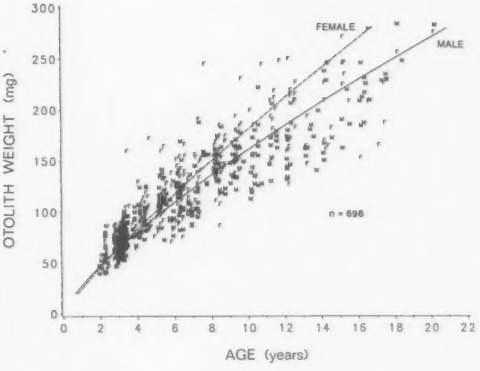


Figure 5
Log-linear growth models by otolith weight for male and female sheepshead. M = male; F = female.

Due to the large variability in age at a given body size, size does not accurately estimate age for sheepshead, especially beyond 2–3 years of age. For example, a given sheepshead greater than 400 mm or 1.5 kg could be of any age from 3 to 20 years.

Otoliths ranged in weight from 28.3 mg (for a 229-mm, 312-g, 2-year-old fish) to 323.5 mg (for a 450-mm, 2410-g, 18-year-old fish). Age-otolith weight (OW) regressions (Fig. 5) were significantly different for males and females ($P<0.0001$ for slopes, $P = 0.0006$ for intercepts); therefore multiple-regression models were fit separately by sex. Dependent variables included in multiple regression models at the 0.10 level of significance were otolith weight and total weight for males, and otolith weight and fork length for females. The addition of any other variables did not significantly improve the fit of the models. The model statistics are presented in Table 2.

Since otolith weight accounted for more of the variability in age (83–85% vs. <60% for fish length or weight), it was the best estimator of age of all morphometric variables considered. However, there was still considerable variability in otolith weight within each age class. Although some of the remaining variability (1–2%) was accounted for by considering fish length or weight in addition to otolith weight, the unexplained variability was great enough that these models could not be used for precise estimation of sheepshead age, such as is needed to determine population year-class structure. However, they could be used to approximate age distribution patterns in the population. In order to obtain precise age estimates of individual fish, otolith annulus counts are necessary.

The linear relationship between otolith weight and age indicates that otolith growth is continuous for sheepshead, whereas fish size (length and weight) asymptotes at intermediate ages and, therefore, is not continuous. This suggests that fast-growing (younger) sheepshead have lighter otoliths than equal-sized slow-growing (older) sheepshead, i.e., otolith growth continues with age, independent of fish growth. This may be a general characteristic of fish growth, as similar observations have been made for other fish species (Templeman and Squires 1956, Beamish 1979, Wilson

Table 2

Regression coefficients and statistics on multiple-regression models of age for sheepshead. Models were fit in a stepwise manner using independent variables of otolith weight, fish standard length, fish total weight, condition factor, and associated interaction terms. Variables were log-transformed for analyses.

Variable	Coefficient	SE	P	Partial r^2
Males (n = 330)				
(1-variable model)				
Intercept = −4.420				
Otolith weight	1.321	0.0305	<0.0001	0.850
(2-variable model)				
Intercept = −3.207				
Otolith weight	1.569	0.0594	<0.0001	0.850
Total weight	−0.331	0.0686	<0.0001	0.010
Females (n = 366)				
(1-variable model)				
Intercept = −3.824				
Otolith weight	1.176	0.0276	<0.0001	0.832
(2-variable model)				
Intercept = 1.258				
Otolith weight	1.484	0.0502	<0.0001	0.832
Fork length	−1.094	0.1531	<0.0001	0.021

and Dean 1983, Radtke et al. 1985, Reznick et al. 1989, Secor et al. 1989). Since fish length or weight accounts for significant variability in age after considering otolith weight, large fish have larger otoliths than equal-aged small fish, i.e., otolith growth is affected by fish growth. These observations support the proposition by Secor and Dean (1989) that not only do otoliths grow in a continuous manner, independent of somatic growth, but also that otolith growth is coupled in some manner to somatic growth.

These growth patterns should be considered when using otoliths for back-calculation of fish size at age. Since continued otolith growth uncoupled from somatic growth would result in slower-growing fish having larger otoliths at a given fish size, the fish-otolith size relationship would be different for fast-growing and slow-growing fish. This bias would be more pronounced at older ages, since otolith growth could continue even if somatic growth has stopped.

Due to gear selectivity and sorting of some samples by fishermen, the age distribution of our samples was not considered to be representative of the Louisiana sheepshead population. Future research should include fishery-independent sampling to accurately characterize the age structure of the sheepshead population, determine variability in recruitment, estimate mortality rates, and identify sources of variability in growth. Additional samples of older fish are required to complete validation of age estimates for the oldest individuals.

Acknowledgments

Sampling efforts were supported by the Louisiana State University's Sea Grant Developmental Program, and the Louisiana Board of Regents. We thank the seafood dealers (including Preston Battistella, Fred and Debbie Black, and Harlon Pearce), tournament organizers, and fishermen for providing samples and facilities. Thanks to Dean Blanchard, David Nieland, Robert Parker, David Stanley, and Bruce Thompson for assistance in data collection.

Citations

Barger, L.E.
1985 Age and growth of Atlantic croakers in the northern Gulf of Mexico, based on otolith sections. Trans. Am. Fish. Soc. 114:847–850.

Beamish, R.J.
1979 New information on the longevity of the Pacific ocean perch (*Sebastes alutus*). J. Fish. Res. Board Can. 36: 1395–1400.

Beamish, R.J., and D.A. Fournier
1981 A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982–983.

Beckman, D.W., C.A. Wilson, and A.L. Stanley
1989 Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the Northern Gulf of Mexico. Fish. Bull., U.S. 87:17–28.

Beckman, D.W., A.L. Stanley, J.H. Render, and C.A. Wilson
1990a Age and growth of black drum in Louisiana waters of the Gulf of Mexico. Trans. Am. Fish. Soc. 119:537–544.

Beckman, D.W., C.A. Wilson, D.L. Nieland, and A.L. Stanley
1990b Age structure, growth rates, and reproductive biology of black drum in the northern Gulf of Mexico. Final report under 1988–1989 U.S. Department of Commerce cooperative agreement NA89WC-H-MF017, Marine Fisheries Initiative (MARFIN) Program. Louisiana State Univ., Coastal Fish. Inst., Baton Rouge, 79 p.

Boehlert, G.W.
1985 Using objective criteria and multiple regression models for age determination in fishes. Fish. Bull., U.S. 83:103–117.

Buxton, C.D., and J.R. Clarke
1986 Age, growth and feeding of the blue hottentot *Pachymetopon aeneum* (Pisces: Sparidae) with notes on reproductive biology. S. Afr. J. Zool. 21:33–38.
1989 The growth of *Cymatoceps nasutus* (Teleostei: Sparidae), with comments on diet and reproduction. S. Afr. J. Mar. Sci. 8:57–65.

Chang, W.B.
1982 A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39: 1208–1210.

Coetzee, P.S., and D. Baird
1981 Age, growth and food of *Cheimerius nufar* (Ehrenberg, 1820) (Sparidae), collected off St Croix Island, Algoa Bay. S. Afr. J. Zool. 16:137–143.

Finkelstein, S.L.
1969 Age and growth of scup in the waters of eastern Long Island. N.Y. Fish Game J. 16:84–110.

Geoghegan, P., and M.E. Chittenden Jr.
1982 Reproduction, movements, and population dynamics of the longspine porgy, *Stenotomus caprinus*. Fish. Bull., U.S. 80:523–540.

Hecht, T., and D. Baird
1977 Contributions to the biology of the pange, *Pterogymnus laniarus* (Pisces: Sparidae): Age, growth and reproduction. Zool. Afr. 12:363–372.

Hildebrand, S.F., and L.E. Cable
1938 Further notes on the development and life history of some teleosts at Beaufort, N.C. Bull. U.S. Bur. Fish. 48:505–642.

Horn, P.L.
1986 Distribution and growth of snapper *Chrysophrys auratus* in the North Taranaki bight, and management implications of these data. N.Z. J. Mar. Freshwater Res. 20:419–430.

Johnson, A.G., W.A. Fable Jr., M.L. Williams, and L.E. Barger
1983 Age, growth, and mortality of king mackerel, *Scomberomorus cavalla*, from the southeastern United States. Fish. Bull., U.S. 81:97–106.

Koranteng, K.A., and T.J. Pitcher
1987 Population parameters, biannual cohorts, and assessment in the *Pagellus bellottii* (Sparidae) fishery off Ghana. J. Cons. Cons. Int. Explor. Mer 43:129–138.

Louisiana Outdoor Writers Association
1987 Official fish records. The Menhaden Advisory Council for the Gulf of Mexico, New Orleans [pamphlet].

Manooch, C.S., and G.R. Huntsman
1977 Age, growth, and mortality of the red porgy, *Pagrus pagrus*. Trans. Am. Fish. Soc. 106:26–33.

NMFS (National Marine Fisheries Service)
1982 Fisheries of the United States, 1981. Current Fish. Stat. 8200, Natl. Mar. Fish. Serv., NOAA, Silver Spring, MD, 131 p.
1990 Fisheries of the United States, 1989. Current Fish. Stat. 8900, Natl. Mar. Fish. Serv., NOAA, Silver Spring, MD, 111 p.

Ott, L.
1988 An introduction to statistical methods and data analysis, 3d ed. PWS-KENT Publ. Co., Boston, 835 p.

Pauly, D.
1980 On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Cons. Int. Explor. Mer 39:175–192.

Pulfrich, A., and C.L. Griffiths
1988 Growth, sexual maturity and reproduction in the hottentot *Pachymetopon blochii* (Val.). S. Afr. J. Mar. Sci. 7:25–36.

Radtke, R.L., M.L. Fine, and J. Bell
1985 Somatic and otolith growth in the oyster toadfish (*Opsanus tau* L.). J. Exp. Mar. Biol. Ecol. 90:259–275.

Reznick, D., E. Lindbeck, and H. Bryga
1989 Slower growth results in larger otoliths: An experimental test with guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. 46:108–112.

Sakamoto, T.
1984 Age and growth of the red sea bream in the outer waters adjacent to the Kii Strait. Bull. Jpn. Soc. Sci. Fish. 50: 1829–1834.

Secor, D.H., and J.M. Dean
1989 Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 46:113–121.

Secor, D.H., J.M. Dean, and R.B. Baldevarona
1989 Comparison of otolith growth and somatic growth in larval and juvenile fishes based on otolith length/fish length relationships. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 191: 431–438.

Sokal, R.R., and F.J. Rohlf
1981 Biometry, 2d ed. W.H. Freeman, San Francisco, p. 459–460.

Springer, V.G., and K.D. Woodburn
1960 An ecological study of the fishes of the Tampa Bay area. Fla. Board Conserv. Mar. Lab. Prof. Pap. Ser. 1, 104 p.

Spurr, A.R.
1969 A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. 26:31–34.

Statistical Analysis Systems
1985 SAS User's Guide: Statistics, Version 5 ed. SAS Inst. Inc., Cary, NC, 956 p.

Templeman, W., and H.J. Squires
1956 Relationship of otolith lengths and weights in the haddock *Melanogrammus aeglefinus* (L.) to the rate of growth of the fish. J. Fish. Res. Board Can. 13:467–487.

von Bertalanffy, L.
1938 A quantitative theory of organic growth. II. Inquiries on growth laws. Hum. Biol. 10:181–213.
1957 Quantitative laws in metabolism and growth. Q. Rev. Biol. 32:217–231.

Waltz, C.W., W.A. Roumillat, and C.A. Wenner
1982 Biology of the whitebone porgy, *Calamus leucosteus*, in the south Atlantic Bight. Fish. Bull., U.S. 80:863–874.

White, M.L., and M.E. Chittenden Jr.
1987 Age determination, reproduction and population dynamics of the Atlantic croaker, *Micropogonias undulatus*. Fish. Bull., U.S. 75:109–123.

Wilson, C.A., and J.M. Dean
1983 The potential use of sagittae for estimating age of Atlantic swordfish, *Xiphias* gladius. *In* Prince, E.D., and L.M. Pulos (eds.), Proceedings of the international workshop on age determination of oceanic pelagic fishes: Tunas, billfishes, and sharks, p. 151–156. NOAA Tech. Rep. NMFS 8.

Wilson, C.A., R.J. Beamish, E.B. Brothers, K.D. Carlander, J.M. Casselman, J.M. Dean, A. Jearld, E.D. Prince, and A. Wild
1987 Glossary. *In* Summerfelt, R.C., and G.E. Hall (eds.), Age and growth of fish, p. 527–530. Iowa State Univ. Press, Ames.

Wilson, C.A., J.H. Render, D.W. Beckman, and A.L. Stanley
1988 The age structure and reproductive biology of sheepshead (*Archosargus probatocephalus*) landed in Louisiana. Final report of funded projects FY 1987–1988, Louisiana Board of Regents' Rockefeller Fund Interest Earnings Grant Program. Louisiana State Univ., Coastal Fish. Inst., Baton Rouge, 49 p.

Wilson, C.A., D.W. Beckman, D.L. Nieland, and A.L. Stanley
1989 Age, growth, and the reproductive biology of schooling red drum from the northern Gulf of Mexico. 1988–1989 final report to Louisiana Department of Wildlife and Fisheries and U.S. Department of Commerce, Marine Fisheries Initiative (MARFIN) Program. Louisiana State Univ., Coastal Fish. Inst., Baton Rouge, 18 p.

Abstract. – Batch fecundity, weight-specific fecundity (number of eggs per gram somatic weight), size of ripe ovarian eggs, and the somatic and gonadal conditions of adult female queenfish *Seriphus politus* were estimated for five spawning seasons during an 8-year (1979–86) period. The effects of female somatic weight were evaluated in analyses of covariance comparing batch fecundity, egg size, and gonadal condition among years.

Batch fecundity was positively (and allometrically) related to female somatic weight. Fecundities were remarkably similar during four of the five years evaluated. After adjustment for annual differences in female size, fecundities were still significantly lower (by about one-fifth) during 1984, a major El Niño year, compared with the preceding (1979–80) or following (1985–86) pairs of years. Gonadal condition also was uniquely low in 1984. The 1984 declines in fecundity and gonadal condition co-occurred with low somatic condition during 1984, particularly for larger females. Mean size (diameter, dry weight) of eggs was indistinguishable among years. There was a positive relation between egg size and female body size, and a general decline in egg size as the spawning season advanced for females of all sizes.

Likely links between declines in fecundity, gonadal and somatic condition, and the crash in planktonic production during the 1982–84 El Niño are discussed.

Manuscript accepted 24 August 1990.
Fishery Bulletin, U.S. 89:9–18 (1991).

Annual Variations in Fecundity, Egg Size, and the Gonadal and Somatic Conditions of Queenfish *Seriphus politus* (Sciaenidae)

Edward E. DeMartini

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396

Few data exist on annual variations in reproductive traits (fecundity, egg size, gonadal allocation) of marine fishes. At a minimum, however, such data are necessary if fisheries ecologists are to begin to understand the many processes, including the vagaries of planktonic transport, that influence the large annual and longer-term temporal fluctuations in the recruitment and subsequent year-class abundance of marine fish stocks (Sinclair 1988, Bailey and Almatar 1989). The influences of egg size and quality on the early growth and survivorship of most species are poorly understood (Ware 1975).

The queenfish *Seriphus politus* is a small croaker abundant in the inner-shelf waters off southern California. It has planktonic egg and larval stages prior to the recruitment of juveniles to epibenthic habitat. Individual females are indeterminate serial spawners that produce as many as 20 batches of eggs during a protracted (6-month) spawning season (DeMartini and Fountain 1981). Juvenile and small adult, including male, queenfish feed on zooplankton (copepods and mysids), and large adults, females in particular, specialize on juveniles of the northern anchovy *Engraulis mordax* (DeMartini et al. 1985).

In this paper, I present data on batch and relative (weight-specific) fecundities, egg size, and the gonadal and somatic conditions of adult female queenfish collected during five spawning seasons spanning an 8-year period from 1979 to 1986. Fecundity, egg size, and condition indices are compared among years and related to concurrent variations in female body size. Because data are available prior to, during, and immediately following a major El Niño event, I interpret my observations in terms of known interannual variations in planktonic production and potential food limitation.

Methods

Sample collection

Queenfish were collected during the March–August reproductive seasons (DeMartini and Fountain 1981) of 1979, 1980, 1984, 1985, and 1986. Nighttime (2000–0200 hours), biweekly to fortnightly collections with a lampara seine, made at 5–16 m bottom depths at three longshore locations in San Onofre–Oceanside waters (DeMartini et al. 1985), were used to index the abundance and to describe the size (length, weight) composition of the nearshore queenfish stock. Sample fish for gonad analyses were provided by daytime lampara seining, otter trawling, and gillnetting at <16-m depths in the same area, and by screenwell samplings of the San Onofre Nuclear Generating Station,

near San Clemente, California. Nighttime samples were used to characterize abundance and size composition, because net avoidance is less at night (Allen and DeMartini 1983). Fish analyzed for reproductive variables and condition were collected during daylight hours, because oocytes destined for imminent spawning are macroscopically recognizable within ovaries only as they hydrate during the half-day preceding dusk spawning (DeMartini and Fountain 1981).

Table 1

Size composition and catch-per-net-haul (CPUE) of adult female queenfish *Seriphus politus* collected during the March–August periods of 1979–86, off northern San Diego County, California. All fish were captured by lampara seines of consistent dimensions, mesh sizes, and method of deployment, during the night at 5–16 m bottom depths (DeMartini and Fountain 1981, DeMartini et al. 1985).

	SL (mm)		Mean somatic	Mean	Number	
Year	$\bar{x}$	% >165 mm	wt (g)	CPUE	Fish	Net hauls
1979	141	19	45	22	872	40
1980	134	16	40	22	995	45
1984	132	2	35	15	294	20
1985	134	6	38	20	624	32
1986	138	7	40	24	948	40

Processing of samples

Queenfish were refrigerated until processed within one day of collection. Sex and maturity were determined from macroscopic characteristics of gonads (DeMartini and Fountain 1981). Adult females were measured (standard length, SL, in mm), and their gonadectomized, wet body weights (as a proxy for somatic weight) were determined to 0.1 g.

Ovary and egg analyses

Both ovaries were removed (fresh) from adult females, weighed damp to 0.01 g, and, for fish in ripe(ning) condition, the presence of hydrated-state oocytes noted based on macroscopic criteria ("Stage 3" ovaries: DeMartini and Fountain 1981).

Hydrated-state ovaries were fixed and preserved in modified Gilson's Fluid (Bagenal and Braum 1971) for about three months, after which declines in oocyte diameters and dry weights should have stabilized (Withames and Walker 1987). These specimens are hereafter referred to as "Gilson's-fixed." Batch fecundity was then determined for a maximum of 10 females per month and year of collection. Fecundity was estimated by gravimetric method (Bagenal and Braum 1971, DeMartini and Fountain 1981). Counts from each section were standardized to the total weight of both ovaries and then averaged (Hunter et al. 1985).

In a subsample of the Gilson's-fixed ovaries, I estimated the median diameter (random axis) of hydrated-state eggs: 10 randomly chosen oocytes per ovary pair were measured within ±25 μm (±1 "eyepiece unit" or "EU") using a compound microscope with ocular micrometer at 40× magnification. I examined a maximum of 10 females per month and year.

A linear dimension such as diameter might not accurately represent egg volume or mass because of variations in chemical composition or density (Blaxter and Hempel 1963). Therefore, I compared the diameter and dry weight of oocytes from Gilson's-fixed ovaries. For 46 females with hydrated-state ovaries present in March–August 1984 collections, I determined the mean dry weight of hydrated oocytes for one member of each ovary pair. I determined the mean diameter of hydrated oocytes for the other member of the ovary pair. Oocyte diameters were measured as described above. I determined mean oocyte dry weight by drying lots of 100 eggs to constant weight (1–2 days) in a vacuum jar over anhydrous calcium chloride. Eggs were dried at room temperature to avoid weight loss of volatiles (Hay 1984, Hislop and Bell 1987), and an aggregate weight determined to the nearest mg on an analytical balance.

Calculation of condition indices

The relative allocation of energy to gonadal tissue was indexed by the RGI of Erickson et al. (1985), as RGI = $(G/W^b) \times 100$, where G = wet weight of ovaries in g, W = wet somatic weight in g, and b = the exponent of the power equation, $G = aW^b$. The relative gonadal index (RGI) is equivalent to $100 \times a$, where a is defined by the linearized (log-transformed) equation, $\ln G = \ln a + b \ln W$ (Erickson et al. 1985). It was necessary to adjust the gonadal index for somatic weight because the slope of the logarithmic gonad-to-somatic weight equation was significantly greater than one (i.e., the relation was allometric).

I first attempted to index somatic robustness as relative somatic condition, $K_n = CW/SL^b$ (Le Cren 1951), where W = wet somatic weight in g, SL = standard length in mm, C = a constant (10^5), and b = the exponent of the regression, $W = aSL^b$. However, the exponent, evaluated as the slope of the log-transformed weight-to-length equation $\ln W = \ln a + b \ln SL$, differed among years, thereby invalidating the use of such an index in analysis of covariance (Erickson et al. 1985,

Cone 1989). I therefore limited my evaluation of robustness to comparisons of estimates of ordinary least-squares regression parameters (Cone 1989).

The relationship between wet and dry body weights might change throughout the spawning season (Love 1970). Therefore, I evaluated seasonal changes in dry somatic weight using 57 females collected at the start of (April–May, $n = 32$) and immediately following (August–September, $n = 25$) the 1985 spawning season. After ovarectomy, fish were frozen in air-tight "zip-lock" bags. Fish were then thawed, and each entire fish was macerated and individually oven-dried to a constant weight at 120°C for 24–32 hours.

Statistical analyses

I used nonparametric analysis of variance (Kruskal-Wallis One-way ANOVA) to compare the body lengths and somatic weights of females among years. Year was evaluated as a fixed-effect class variable, because I was interested in evaluating potential differences among a preestablished series of years. Analysis of covariance (ANCOVA) was used whenever possible to evaluate the effects of sampling year on batch fecundity, and on relative gonadal condition, after adjustment for year differences in somatic weight. A two-way Model I ANCOVA was used to evaluate subseasonal (approximately bimonthly) influences of egg diameter among years for females of differing body lengths. Dry egg weight was related to egg diameter by parametric regression. Dry somatic weight was regressed on wet weight for sample fish collected at the beginning and at the end of the 1985 spawning season; regressions were then compared using ANCOVA with body length as the covariate. Computations were made using the GLM, REGRESS and TTEST software procedures of the Professional Database Analysis System (PRODAS; Conceptual Software Inc. 1986).

Table 2

Summary statistics for adult female queenfish *Seriphus politus* used in analyses of reproductive variables and condition. Gonadal condition (RGI), batch fecundity, and egg diameter variables are least-square means (adjusted for annual differences in the body-size covariate). All variables, including fecundity, refer to sample females only. See Methods for explanations of the covariate used to adjust particular variables. One standard error is given in parentheses below each mean.

Year	*N*	SL (mm)	Somatic weight (W, g)	RGI[a]	Batch fecundity[b] (no. eggs)	Egg diameter[c] (EU)
1979	44	165	77	3.8	14,752	19.10
		(5)	(7)	(.2)	(1)	(.18)
1980	126	151	56	4.7	15,019	20.61
		(2)	(3)	(.1)	(1)	(.18)
1984	71	137	37	3.9	11,784	20.11
		(2)	(1)	(.2)	(1)	(.23)
1985	77	141	44	5.3	14,550	21.03
		(2)	(2)	(.2)	(1)	(.18)
1986	75	143	44	4.1	14,199	21.10
		(2)	(2)	(.2)	(1)	(.18)

[a] Estimates (± SE) of the exponent "b" in the power equation, gonad weight (G) = aW^b, were 1.185 ± 0.092 (in 1979), 1.162 ± 0.053 (1980), 1.232 ± 0.124 (1984), 1.280 ± 0.102 (1985), and 1.011 ± 0.102 (1986). Estimates did not differ among years, and were consistently greater than one (ANCOVA; ln somatic W × Yr interaction: $F_{4,383} = 0.87$, $P = 0.48$; pooled slope = 1.1810.

[b] Batch fecundity estimates were back-calculated from the means and SE's of ln-transformed data, multiplied by the correction factor of Sprugel (1983).

[c] Using the largest size-class of oocytes (ripe, hydrated-state) present in Gilson's-fixed ovaries (see Methods).

Results

Variations in female body size and CPUE

The size composition of the nearshore, adult female queenfish stock differed among years. Mean female length and weight were significantly lower in 1985 and especially 1984 (Kruskal-Wallis one-way ANOVA; both $P<0.001$). Large females (≥165 mm SL, chosen because they were relatively rare during 1984–86) in fact were nearly absent in 1984, when overall mean female abundance was at an estimated low (Table 1).

Females used in analyses of reproduction and condition also differed in mean body size (both somatic weight and length) among sample years (Kruskal-Wallis ANOVA, both $P<0.001$; Table 2).

Dry vs. wet somatic weight

The dry somatic weight of female queenfish averaged 24% of wet weight for fish collected at the beginning and at the end of the 1985 spawning season. Body length obviously influenced dry weight; subseason, however, had no significant effect on dry weight (ANCOVA of effects of body length and subseason on dry weight: length effect—$F_{1,54} = 346$, $P<0.0001$; subseason effect—$F_{1,54} = 0.42$, $P = 0.52$). Wet weight, therefore, could be used as an accurate proxy for dry weight throughout the queenfish spawning season, once adjusted for variations in female body size.

Batch fecundity

Batch fecundity in queenfish was positively related to female body size in each year (Table 3; Fig. 1). Fecundity was generally better related (based on higher R^2 values) to somatic weight than body length. Batch fecundity was disproportionately large in heavier females, as indicated by the value of the slope in the linear double-log plot (Fig. 1). Fecundity also differed among years, even after adjustment for annual differences in female size, with mean fecundity in 1984 significantly lower (by 20%) than mean fecundity in the other four years (Tables 2, 3, 5; Fig.1).

Table 3

Summary of ANCOVAs[a] testing the effects of female somatic weight and year on batch fecundity (F, no. eggs) and relative gonadal index (RGI). Both model R^2 are significant at $P<0.001$ (ln F, $R^2 = 0.694$; RGI, $R^2 = 0.114$).

Dependent variable	Source	df	*SS*	*MS*	*F*	*P*
ln F	ln W	1	118.1	118.1	693	<0.0001
	Yr	4	3.4	0.8	4.9	<0.0001
	Error	387	65.9	0.2		
RGI	ln W	1	0.06	0.06	0.03	0.87
	Yr	4	111	27.7	12.5	<0.0001
	Error	387	860	2.2		

[a]ln W × Yr interaction terms deleted for analysis of ln F ($P = 0.61$) and for analysis of the RGI ($P = 0.84$).

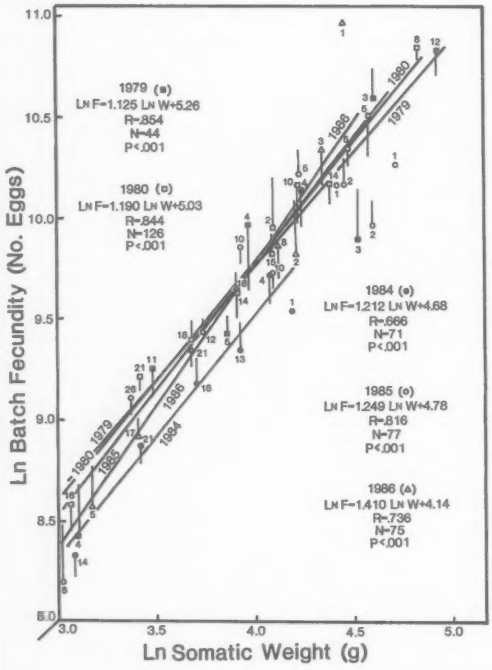


Figure 1

Relationship between the log of batch fecundity (ln F) and log female somatic weight (ln W) during each of the five study years. For illustration, mean fecundity data (+1 SE) are plotted for each 10-g weight class. The allometric equation, $F = aW^b$ (in log-linear form as $\ln F = \ln a + b \ln W$), and its summary statistics are provided for each fitted regression line.

Weight-specific fecundity

Patterns of weight-specific fecundity (WSF, no. eggs per g somatic weight) resembled those of batch fecundity. WSF appeared to increase with female body weight (ANCOVA of effects of somatic weight and year on WSF: weight effect—$F_{1,387} = 13.1$, $P<0.001$), and also seemed to vary among years ($F_{4,387} = 2.84$, $P = 0.025$). However, main effects were confounded by a weakly significant weight-by-year interaction ($F_{4,387} = 2.57$, $P = 0.038$). This heterogeneity of slopes prevented adjustments for annual variations in female weight and invalidated comparisons of intercepts among all five years. Although WSF generally increased with body weight, the disproportionate effect of larger females varied among years. Most notable was the particularly strong, positive influence of somatic weight on WSF in 1986. If the 1986 data are deleted and the ANCOVA analysis rerun, the slope heterogeneity disappears ($F_{3,310} = 0.82$, $P = 0.49$). When main effects are reanalyzed, a strong year effect ($F_{3,313} = 6.02$, $P<0.001$) becomes apparent, in addition to that of somatic weight. This year effect disappears ($F_{3,243} = 0.56$, $P = 0.57$) if the 1984 data are removed. Size-adjusted WSF in 1984 (mean ± SE = 264 ± 15 eggs per g) clearly was less than that in 1979, 1980, and 1985 (336 ± 8 eggs per g).

Diameter vs. dry weight of eggs

The median diameter of Gilson's-fixed, hydrated-state eggs was significantly related to the mean dry weight of these eggs (dry weight [in g, $\times 10^{-6}$] = 7.2 + 0.4931 egg diameter; $r = 0.47$, $n = 46$ females, $P = 0.001$). The mass of hydrated-state eggs therefore was approximately predicted ($R^2 = 0.22$) by egg diameter. While appropriate, I acknowledge that a more direct and

accurate measurement of egg mass would have been preferable.

Egg size

Egg size varied with female body length and period within spawning season, with larger eggs produced by larger females, and all females producing larger eggs earlier in the season (Table 4; Fig. 2). The mean size of eggs did not vary among years, after adjustments for annual differences in female size and a significant period × year interaction (Tables 4,5). The latter interaction illustrates that the pattern of subseasonal decline in egg size varied among years (Fig. 2). Adjusted for female length, mean egg diameter appeared to vary 10% among years (Table 2). This difference in egg diameters, expressed in terms of volume (as 4/3 πr^3, the volume of a sphere), was 35% of the smaller value.

Table 4

Results of two-way ANCOVA testing the effects of female body length (SL, as covariate), study year (spawning season), and bimonthly period within the spawning season on size of ripe ovarian eggs. See Methods for explanation of egg size measurements. Model R^2 (0.510) significant at $P<0.001$.

Dependent variable	Source	df	*SS*	*MS*	*F*	*P*
Egg diameter	SL	1	57	57.0	22.5	<0.0001
	Period	2		{inestimable}		
	Yr	4		{inestimable}		
	Period × Yr	8	226	28.2	11.2	<0.0001
	Error	372	942	2.5		

Table 5

Summary of a posteriori Bonferroni *t*-tests for identity of year effects detected by ANCOVAs summarized in Tables 3 and 4. Means connected by underlines are not significantly different at $P = 0.05$. See Table 2 for values of adjusted means and SEs.

Variable	Year contrasts
ln F	1984 < 1985 = 1986 < 1980 < 1979
Egg diameter	1979 = 1984 = 1980 = 1985 = 1986
RGI	1979 = 1984 = 1986 < 1980 = 1985

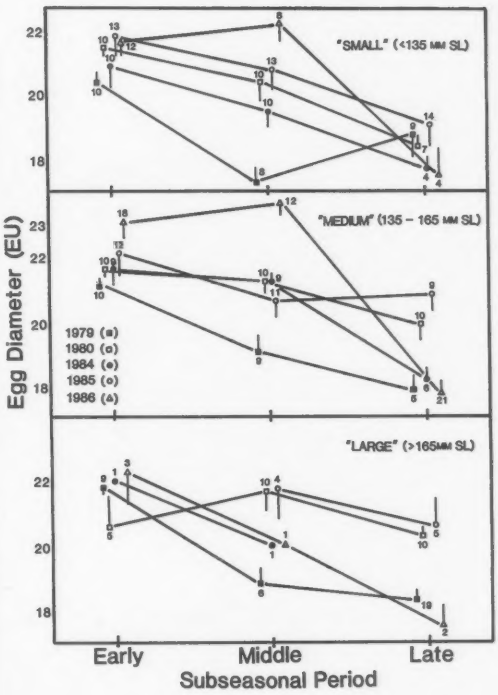


Figure 2

Relationship between mean (±1 SE) egg size (diameter of Gilson's-fixed, hydrated oocytes) and bimonthly period within spawning season for female queenfish of three arbitrary body sizes (small ≤13.5 cm, medium 13.6–16.5 cm, and large ≥16.5 cm SL), by sample year. See Tables 4 and 5 for results of ANCOVA testing the effects of subseasonal period (within year) on egg size, with female body lengths evaluated as a covariate. Data were pooled by bimonthly period to increase sample sizes.

Condition indices

Somatic condition varied with body size. Larger females usually were more robust (Table 6), but somatic condition also varied among years; the slopes and intercepts of length–weight relations were lower in 1984 and 1985 than in the other three years (Table 6). Larger females in particular were less robust in 1984 and 1985 (i.e., there was a highly significant ln SL × year interaction; Table 6), and this invalidated a straightforward interpretation of the effects of body size and year on a summary index of somatic condition.

As indicated by values consistently greater than one for the exponent "b" in the equation, $G = aW^b$, percentage gonad-to-somatic weight allocation increased for larger females (Table 2; Fig. 3). However, relative

gonadal condition, as described by the RGI of Erickson et al. (1985) in which gonad weight has been standardized by female somatic weight, did not vary with female size (Table 3). The RGI did differ among years in concert with size-adjusted variations in fecundity; mean RGI in 1984 was about 14% lower than the RGI averaged over the other four years (Tables 2, 5). An identical pattern of annual variation in gonadal condition is observed if the classical gonadal index (GSI = [G/W] × 100) is used as the dependent variable in ANCOVA instead of the RGI.

Table 6

Least-squares regression parameters for length-weight relationships of adult female queenfish in each[a] of the study years. Ordinary least-squares regressions were calculated for the double-log transformed equation, $\ln W = \ln a + b \ln SL$, where ln a is the intercept and b is the slope.

	Intercept		Slope				
Year	Estimate	SE	Estimate	SE	R^2	N	P
1979	−11.864	0.246	3.151	0.048	0.990	44	<0.0001
1980	−11.660	0.178	3.106	0.036	0.984	126	<0.0001
1984	−10.450	0.378	2.853	0.077	0.952	71	<0.0001
1985	−10.433	0.206	2.862	0.042	0.984	77	<0.0001
1986	−11.888	0.616	3.152	0.124	0.898	75	<0.0001

[a]Estimated slopes of the ln W – ln SL relations differed among years (ANCOVA; ln SL × Yr interaction: $F_{4,393} = 6.10$, $P < 0.0001$).

Potential biases of condition indices

These differences in somatic and gonadal conditions were not the result of year variations in condition-selective collection methods. Lampara-seined fish comprised 84–100% of the specimens examined for condition in each year; among non-lampara fish, a maximum of 14% of the fish examined (in 1984) were collected by otter trawl. The somatic conditions ($K = 10^5 W/SL^3$; Le Cren 1951) of fish collected by lampara seine and otter trawl during April–June 1984, the only period when testable numbers of fish were collected using more than one method, were indistinguishable (seine: mean ± SE condition = 1.40 ± 0.016; trawl: mean ± SE = 1.39 ± 0.010; Student's $t = 0.28$, df = 151, $P = 0.78$).

Discussion

Annual variations in body size

Interannual variations in the body size of adult female queenfish were marked, with the percentage contribution of large fish varying tenfold and mean somatic weights of the nearshore female stock varying by 25% over the study period. Clearly, potential year effects on fecundity and other size-sensitive variables are confounded with the effects of annual variations in body size, necessitating the use of size as a covariate in analyses.

Fecundity and female body size

During each of the queenfish spawning seasons monitored, batch fecundity was positively related to female body size, especially somatic weight. The overall mean value of b in the equation, $F = aW^b$ was 1.2087, which is significantly greater than unity.

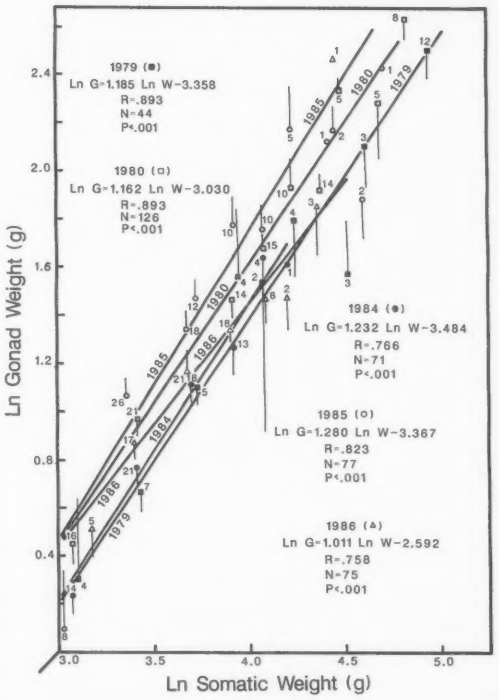


Figure 3

Relationship between the log of ovary weight (ln G) and log female somatic weight (ln W) during each of the five study years. For illustration, mean ovary weight data (+1 SE) are plotted for each 10-g weight class. The equation, $G = aW^b$ (in log-linear form as $\ln G = \ln a + b \ln W$), and its summary statistics are provided for each fitted regression line.

In another detailed study, Parrish et al. (1986) detected allometric weight-specific fecundities in a size-(age-) structured stock of the northern anchovy. Empirical data for additional species of "weedy" (fast-growing, high-fecundity) fishes suggest that allometric fecundity-weight relations may be a general phenomenon (Blaxter and Hunter 1982, Clarke 1987). Reiss (1987), in a review and interpretation of relevant data, calculated that larger (older) fish in general have disproportionately large reproductive investments. Williams (1966), Wootton (1979), and Reiss (1987) have argued that disproportionate investments by older individuals should be adaptive for many iteroparous fishes with indeterminate growth. The queenfish data further suggest that allometry in gonadal allocation may be more common than is generally appreciated. Adjustments for allometry are required when calculating egg-based stock size estimates for species like queenfish and northern anchovy (Parrish et al. 1986).

Covariates of egg size

Egg size was positively related to queenfish body length, but declined for females of all sizes as water temperatures increased between the beginning (March–April) and end (July–August) of the spawning season. Egg size has been observed to increase with female body size, and decreases in egg size have been related to increases in water temperature during spring–summer production cycles, for diverse marine fishes (Williams 1967, Ware 1977, Blaxter and Hunter 1982 and references, Kashiwagi et al. 1985, Knutsen and Tilseth 1985, Daoulas and Economou 1986 and references, Imai and Tanaka 1987, Tanasichuk and Ware 1987). A positive female size–egg size relation and a seasonal decline in egg size with increasing water temperatures, the latter either ecophenotypic or genetic responses to the changing prey or predator (Clarke 1989) spectra confronting larvae, are now recognized as general phenomena in marine pelagic-spawners (Ware 1975; Markle and Frost 1985). It is obvious that estimates of mean egg size (and fecundity) must account for the effects of female body size and subseasonal variation.

Annual variations in fecundity and egg size

Batch fecundities of queenfish (adjusted for annual variations in female size) varied less than 6% during four out of the five years of this study. A marked change in batch fecundity, after adjustments for variations in female size, occurred only in 1984. Weight-specific fecundities paralleled batch fecundities.

Queenfish egg size varied little among the five years studied. Apparent egg volume averaged about 24% smaller in 1979 than during the other four years.

Few data exist on annual variations in the egg production of marine fishes (Bagenal 1957 and references, Antony Raja 1971, Pinhorn 1984, Hunter et al. 1985, Bailey and Almatar 1989). As one might expect, the size-specific fecundity of individuals varies among years, but sometimes fecundities are remarkably similar within a short series of years (Antony Raja 1971, Pinhorn 1984, Hunter et al. 1985). Observational and experimental studies (e.g., Tyler and Dunn 1976, Wootton 1979, Hunter and Leong 1981, Hay and Brett 1988) demonstrate that fluctuations in fecundity can and do result from naturally occurring food limitation. Food rations can also affect egg size (Hislop et al. 1978, Le Clus 1979). The trivial inference is that food can sometimes, although not invariably, limit egg production. Of greater interest is that, for queenfish, the maximum observed deviation from long-term average fecundity was only a 20% decline in a single year of unique oceanographic conditions, as described in the following section.

El Niño effects

The anomalously low fecundities and somatic condition of queenfish in 1984 occurred at a time when the 1982–84 El Niño was still evident in the Southern California Bight (McGowan 1985). During 1983–84, zooplankton production was at unusually low levels in inner-shelf waters (Petersen et al. 1986), mirroring the nadir in phyto- and zooplankton production in the California Current, farther offshore (McGowan 1985). This decline in planktonic production off southern California lagged the more extreme declines in production that resulted from the parent El Niño that occurred off the western coast of South America during 1982–83 (Barber et al. 1985).

During the 1982–84 California El Niño, tropical pelagic fishes migrated northward; many species became abundant off southern California, with some noted as far north as Washington–British Columbia (Smith 1985, Mysak 1986). El Niño effects on subtropical and cold-temperate fishes are poorly understood. Bailey and Incze (1985) and Mysak (1986) summarized the fragmentary data then available on distributional shifts and fluctuations in stock sizes of temperate fishes. Bailey and Incze (1985) speculated that El Niño effects on water temperature, nutrients, and planktonic production could effect egg and larval physiologies, disrupt the transport of early-life-history stages, and impact the somatic condition and egg production of adults. For vagile species, major impacts such as these should prompt movements to regions more favorable for growth and reproduction (Bailey and Incze 1985).

My data on interannual variations in body size composition suggest that large female queenfish (those individuals whose somatic condition and reproduction were particularly stressed by reductions in their anchovy prey) responded to El Niño conditions in part by emigrating out of the study area. The observed 1984 nadir in females >165 mm, followed by the return of fish of this size in 1985–86, demonstrates that emigration had to have occurred, because 165-mm long queenfish are more than 3 years-old (E. DeMartini, unpubl. data). Large fish might have emigrated to deeper depths, tracked colder water masses upcoast, or done both; unfortunately, lack of data prevent discrimination among these possibilities.

The only published evidence thus far for El Niño effects on adult fish condition and egg production off the west coast of North America are for the central stock of the northern anchovy (Fiedler et al. 1986), yellowtail rockfish *Sebastes flavidus* (Lenarz and Echeverria 1986), and for Pacific herring *Clupea harengus pallasi* (Tanasichuk and Ware 1987). In anchovy, individual egg production was lower in 1983–84 than in 1980–82 and 1985; this reflected lower spawning frequencies more than declines in batch fecundity (Fiedler et al. 1986). Specific fecundity (the daily production of eggs per unit biomass) of anchovy was low in 1983 (although high in 1984, the second El Niño year) compared with other years between 1980 and 1985. Growth rates of juvenile–adult anchovy were low in 1983–84 (Fiedler et al. 1986). For yellowtail rockfish off the central California coast, the visceral fat and gonad volumes of adults were lower in 1983 than in 1980 (Lenarz and Echeverria 1986). Off British Columbia, Pacific herring responded to the El Niño with increased batch fecundities coincident with reductions in mean egg size (Tanasichuk and Ware 1987). Adults of the anchovy and rockfish do not regularly occur in inner-shelf waters: most anchovy frequent the California Current, tens to several hundred kilometers offshore of central and southern California. Adult yellowtail rockfish are an epibenthic predator of continental borderlands offshore of the coasts of British Columbia–California.

It is tempting to speculate that the observed decrease in fecundity and somatic condition of queenfish during 1984 reflects lower production of the planktonic and anchovy prey of adults during a major El Niño year, compared with the 1979–80 and 1985–86 periods. If true, these data are among the first to show annual variations in egg production resulting from differences in size-specific batch fecundity, rather than changes in the duration of the spawning season or changes in the spawning frequency of females (Hunter et al. 1985). Interestingly, queenfish egg mass was not detectably lower in 1984, concurrent with the 20% decline in the number of eggs produced per batch, so the impact on egg production may have involved only the quantity, not the quality of eggs. Total number of spawnings per female season, whether due to changes in the duration of the spawning season or frequency of spawning by individual females, also might have varied for queenfish during 1979–86, but data are lacking. Length of spawning season and the interval between batches are unlikely to cancel out the batch fecundity pattern, though, since they might be expected to vary in concert with fecundity, if they covary at all (Hunter et al. 1985).

My observations also provide one of the first suggestions of food web impacts of the 1982–84 California El Niño on an inner-shelf fish species. Unfortunately, data on potential El Niño effects on the survivorship of early-life stages and year-class establishment are lacking for queenfish, as for offshore fishes. Future studies should concurrently measure survivorship and recruitment, together with population fecundity and egg production of the stock, in addition to individual fecundity and condition.

Acknowledgments

Many skilled technicians assisted in the collection of sample fish and in dissecting and processing ovaries. I especially thank S. Garner, K. George, G. Greenwald, and D. Opalenik. Special thanks go to R. Fountain, without whose diligent notekeeping this study would not have been possible. Also gratefully acknowledged are the constructive criticisms of T. Present and E. Schultz on drafts of the manuscript. Two anonymous reviewers contributed substantially to the improvements of draft manuscripts. This study was done in conjunction with complementary work funded by the Marine Review Committee, Inc., of the California Coastal Commission, and I thank the Committee for their support.

Citations

Allen, L.G., and E.E. DeMartini
1983 Temporal and spatial patterns of nearshore distribution and abundance of the pelagic fishes off San Onofre–Oceanside, California. Fish. Bull., U.S. 81:569–586.

Antony Raja, B.T.
1971 Fecundity fluctuations in the oil sardine *Sardinella longiceps* Val. Indian J. Sci. 18:84–98.

Bagenal, T.B.
1957 Annual variations in fish fecundity. J. Mar. Biol. Assoc. U.K. 36:377–382.

Bagenal, T.B., and E. Braum
1971 Eggs and early life history. *In* Ricker, W.E. (ed.), Methods for assessment of fish production in fresh waters, p. 166–198.

IBP (Int. Biol. Prog.) Handb. 3, Blackwell Sci. Publ., Oxford.

Bailey, K.M., and L.S. Incze
1985 El Niño and the early life history and recruitment of fishes in temperate marine waters. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean, p. 143–165. Wash. Sea Grant Prog., Univ. Wash., Seattle.

Bailey, R.S., and S.M. Almatar
1989 Variation in the fecundity and egg weight of herring (*Clupea harengus* L.). Part II. Implications for hypotheses on the stability of marine fish populations. J. Cons. Cons. Int. Explor. Mer 45:125–130.

Barber, R.T., J.E. Kogelschatz, and F.P. Chavez
1985 Origin of productivity anomalies during the 1982–83 El Niño. Calif. Coop. Oceanic Fish. Invest. Rep. 26:65–71.

Blaxter, J.H.S., and G. Hempel
1963 The influence of egg size on herring larvae (*Clupea harengus* L.). J. Cons. Cons. Int. Explor. Mer 28:211–240.

Blaxter, J.H.S., and J.R. Hunter
1982 The biology of the clupeoid fishes. Adv. Mar. Biol. 20: 1–223.

Clarke, T.A.
1987 Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish. Bull., U.S. 85:127–138.
1989 Seasonal differences in spawning, egg size, and early developmental time of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish. Bull., U.S. 87:593–600.

Conceptual Software, Inc.
1986 PRODAS database, statistics, graphics: Manual and user's guide. Conceptual Software, Inc., Houston, Texas.

Cone, R.S.
1989 The need to reconsider the use of condition indices in fishery science. Trans. Am. Fish. Soc. 118:510–514.

Daoulas, C., and A.N. Economou
1986 Seasonal variation of egg size in the sardine, *Sardina pilchardus* Walb., of the Saronikos Gulf: Causes and probable explanation. J. Fish Biol. 28:449–457.

DeMartini, E.E., and R.K. Fountain
1981 Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: Attributes representative of serial spawning fishes. Fish. Bull., U.S. 79:547–560.

DeMartini, E.E., L.G. Allen, R.K. Fountain, and D. Roberts
1985 Diel and depth variations in the sex-specific abundance, size composition, and food habits of queenfish, *Seriphus politus* (Sciaenidae). Fish. Bull., U.S. 83:171–185.

Erickson, D.L., J.E. Hightower, and G.D. Grossman
1985 The relative gonadal index: An alternative index for quantification of reproductive condition. Comp. Biochem. Physiol. 81A:117–120.

Fiedler, P.C., R.D. Methot, and R.P. Hewitt
1986 Effects of the California El Niño 1982–1984 on the northern anchovy. J. Mar. Res. 44:317–338.

Hay, D.E.
1984 Weight loss and change of condition factor during fixation of Pacific herring, *Clupea harengus pallasi*, eggs and larvae. J. Fish Biol. 25:421–433.

Hay, D.E., and J.R. Brett
1988 Maturation and fecundity of Pacific herring (*Clupea harengus pallasi*): An experimental study with comparisons to natural populations. Can. J. Fish. Aquat. Sci. 5:399–406.

Hislop, J.R.G., and M.A. Bell
1987 Observations on the size, dry weight and energy content of the eggs of some demersal fish species from British marine waters. J. Fish Biol. 31:1–20.

Hislop, J.R.G., A.P. Robb, and J.A. Gauld
1978 Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglefinus* (L.) in captivity. J. Fish Biol. 13:85–98.

Hunter, J.R., and R. Leong
1981 The spawning energetics of female northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:215–230.

Hunter, J.R., N.C.H. Lo, and R.J.H. Leong
1985 Batch fecundity in multiple spawning fishes. *In* Lasker, R. (ed.), An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*, p. 67–77. NOAA Tech. Rep. NMFS 36.

Imai, C., and S. Tanaka
1987 Effect of sea water temperature on egg size of Japanese anchovy. Bull. Jpn. Soc. Sci. Fish. 53:2169–2178.

Kashiwagi, M., F. Nakamura, T. Okada, and N. Yamada
1985 A periodic variation of egg size of Japanese whiting *Sillago japonica* during the spawning season. Aquiculture 33:134–138.

Knutsen, G.M., and S. Tilseth
1985 Growth, development, and feeding success of Atlantic cod larvae *Gadus morhua* related to egg size. Trans. Am. Fish. Soc. 114:507–511.

Le Clus, F.
1979 Dry mass of yolked oocytes of the South West African pilchard *Sardinops ocellata* in relation to maturity stages and spawning cycles, 1972–1974. S. Afr. Sea Fish. Branch Invest. Rep. 119, 29 p.

Le Cren, E.D.
1951 The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. 20:201–219.

Lenarz, W.H., and T.W. Echeverria
1986 Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. Fish. Bull., U.S. 84:743–745.

Love, R.M.
1970 The chemical biology of fishes. Academic Press, London.

Markle, D.F., and L.-A. Frost
1985 Comparative morphology, seasonality, and a key to planktonic fish eggs from the Nova Scotian Shelf. Can. J. Zool. 63:246–257.

McGowan, J.A.
1985 El Niño 1983 in the Southern California Bight. *In* Wooster, W.S., and D.S. Fluharty (eds.), El Niño north: Niño effects in the eastern subarctic Pacific Ocean, p. 166–187. Wash. Sea Grant Prog., Univ. Wash., Seattle.

Mysak, L.A.
1986 El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43:464–497.

Parrish, R.H., D.L. Mallicoate, and R.A. Klingbeil
1986 Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 84:503–518.

Petersen, J.H., A.E. Jahn, R.J. Lavenberg, G.E. McGowen, and R.S. Grove
1986 Physical-chemical characteristics and zooplankton biomass of the continental shelf off southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:36–52.

Pinhorn, A.T.
1984 Temporal and spatial variation in fecundity of Atlantic cod (*Gadus morhua*) in Newfoundland waters. J. Northwest Atl. Fish. Sci. 5:161–170.

Reiss, M.J.
1987 The intraspecific relationship of parental investment to female body weight. Functional Ecol. 1:105–107.

Sinclair, M.
1988 Marine populations: An essay on population regulation and speciation. Wash. Sea Grant Prog., Univ. Wash. Press, Seattle, 252 p.

Smith, P.E.
1985 A case history of an anti-El Niño to El Niño transition on plankton and nekton distribution and abundances. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean, p. 121–142. Wash. Sea Grant Prog., Univ. Wash., Seattle.

Sprugel, D.G.
1983 Correction for bias in log-transformed allometric equations. Ecology 64:209–210.

Tanasichuk, R.W., and D.M. Ware
1987 Influence of interannual variations in winter sea temperature on fecundity and egg size in Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 44:1485–1495.

Tyler, A.V., and R.S. Dunn
1976 Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding homeostasis. J. Fish. Res. Board Can. 33:63–75.

Ware, D.M.
1975 Relation between egg size, growth, and natural mortality of larval fish. J. Fish. Res. Board Can. 32:2503–2512.
1977 Spawning time and egg size of Atlantic mackerel, *Scomber scombrus*, in relation to the plankton. J. Fish. Res. Board Can. 34:2308–2315.

Williams, G.C.
1966 Adaptation and natural selection. Princeton Univ. Press, Princeton, 307 p.
1967 Identification and seasonal size changes of eggs of the labrid fishes, *Tautogolabrus adspersus* and *Tautoga onitis* of Long Island Sound. Copeia 1967:452–453.

Witthames, P.R., and M.G. Walker
1987 An automated method for counting and sizing fish eggs. J. Fish Biol. 30:225–235.

Wootton, R.J.
1979 Energy costs of egg production and environmental determinants of fecundity in teleost fishes. Symp. Zool. Soc. Lond. 44:133–159.

Age, Growth, and Structure of Vertebra in the School Shark *Galeorhinus galeus* (Linnaeus, 1758) from Southern Brazil

Beatrice Padovani Ferreira

Fundacao Universidade do Rio Grande, Rio Grande, RS, 96200, Brazil
Present address: Marine Biology Department
James Cook University of North Queensland, Townsville Q4811, Australia

Carolus Maria Vooren

Departamento de Oceanografia, Fundacao Universidade do Rio Grande
Rio Grande, RS, 96200, Brazil

Abstract.– Age and growth of the school shark *Galeorhinus galeus* was studied from rings in the vertebra and length-frequency data. Samples were collected by trawling off the southern Brazilian coast from June 1980 to September 1986. Histological studies were also conducted on the characteristics of the vertebra. Standard histological techniques and microradiography were used to determine the pattern of vertebral calcification. The vertebrae of *G. galeus* are composed of calcified cartilage. Chondrocytes in calcified zones remain alive, probably nourished through vascular channels extending from the perichondrium into the cartilage matrix. A narrow zone of uncalcified matrix at the outer edge of the centrum indicates that calcification is preceded by initial development of hyaline cartilage. The vertebra presents a pattern of alternating heavily and less heavily mineralized zones, narrow and wide, respectively. The narrow zones were named rings, which are translucent under transmitted light and white to the microradiograph. These rings are probably laid down yearly in a slow-growing phase extending throughout the four winter months of June to September. Lengths at age were back-calculated and the von Bertalanffy growth parameters are: males—$K = 0.092$, $L_\infty = 152$ cm, and $t_0 = -2.69$; females—$K = 0.075$, $L_\infty = 163$ cm, and $t_0 = -3.00$. ELEFAN software was used to determine the growth curve best fitted to length-frequency data, but results overestimated the growth rate due to the slow growth and modal overlap.

Manuscript accepted 12 October.
Fishery Bulletin, U.S. 89:19–31 (1991).

The elasmobranch skeleton consists of calcified cartilage. In most elasmobranchs, vertebrae are the only available structure that display periodic rings, which are useful for determining age. These rings result from different ratios of organic matrix/mineral, making the zones optically distinct (Casselman 1974). Since the description by Ridewood (1921), several techniques have been developed for enhancing the visibility of these rings thus making the counts easier and more accurate. However, information about the histology of elasmobranch vertebral rings is limited, and statements about their chemical composition and optical properties are contradictory (Casselman 1983).

The school shark *Galeorhinus galeus* is one of the principal species in the shark fishery in southern Brazil (Vooren and Betito In press). With the purpose of providing information for management decisions, age and growth of the Brazilian school shark were determined from rings in the vertebrae and length-frequency data. A histological study was conducted to investigate the structure of the vertebrae and to determine variations in their composition.

Materials and methods

The study area was the continental shelf and upper slope off southern Brazil, between latitudes 34° and 30°S, at depths between 10 and 500 m. Data used for size-frequency analysis were obtained during trawl fisheries of this area from June 1980 to September 1986 (Table 1). All fishes were sexed and their total length (TL, cm) was measured from the tip of the snout to the extremity of the upper lobe of the tail, which was stretched back to be aligned with the body axis. Vertebrae were collected during the cruises listed in Table 1, and samples were chosen to include both sexes and the full size-range available. Sexual maturity and reproductive stage (Table 2) were determined according to size criteria established for this species by Peres (1989).

The data were processed on the Statistical Package for the Social Sciences, SPSS (Nie 1975). Length-frequency distributions for both sexes were plotted by cruise, by month, and also by a selected combination of the two largest samples. The ELEFAN (Electronic Length Frequency Analysis) software (Pauly and David 1981) was used to determine growth parameters (k and L_∞) from length-frequency data. The goodness of fit was given by the index Rn.

Vertebrae for age determination were dissected in the field from the

region under the first dorsal fin. The vertebrae were cleaned, frozen, and preserved in 70% ethanol. Several techniques were tried to aid enhancement and interpretation of the vertebral rings. Vertebrae of 10 sharks were sectioned into two halves, through transverse or sagittal planes, and the exposed faces were polished on wet 600-grit sandpaper. They were decalcified in 1% formic acid for 1 hour, rinsed in running water for 24 hours, dried and stained with graphite powder. The material was observed with a dissection microscope at 10× magnification using reflected light.

Vertebrae from 82 individuals (35 males, 45 females, and 2 embryos) were dehydrated in ethanol, cleared in styrene, embedded in polyester resin, sectioned with a jeweller's saw in transverse and sagittal planes, and polished on wet 400-grit sandpaper to obtain slices of 50–250 microns. Radiographs of all sections were taken with Soft X-ray equipment by Moureuil (France), at settings of 10–30 kV, 5–15 mA, and exposure times of 3–5 minutes. Kodak Industrex M radiography film was used. The radiographs were mounted on glass slides as were vertebra sections, either directly or after staining with Harris's haematoxylin or basic fuchsin. Vertebrae from five sharks were prepared and sectioned by standard histological techniques for calcified material. Sections were stained with Sudan 4 for observation of the lipid contents of cells.

A dissecting microscope at 10× magnification was used for measuring and counting growth rings, and a compound microscope at 100× magnification for observation of cell structure and details of the margin of the vertebra. The criteria to define a ring requires that it must occupy a distinct translucent zone relative to adjacent opaque zones and that the ring traverse the corpus calcareum and intermedialia (modified from Casey et al. 1985).

Measurements of growth increments were made with an ocular micrometer positioned to measure distances from the focus (notochordal remnant) to successive growth bands. The radius of each centrum was measured from the focus to the distal margin of the corpus calcareum (Fig. 1). The widths of individual translucent and opaque zones were measured in the microradiographs of 10 individuals. The periodicity of the formation of the rings was studied by examining the margins of the vertebrae collected from June to September. The marginal zone was classified into three types: pre-ring, consisting of a wide, less calcified zone; ring, consisting of a more calcified zone; and post-ring, consisting of a narrow, less calcified zone. Measurements of marginal increments were considered to be ineffective because the widths of zones varied greatly between size classes.

A linear regression of TL as a function of centrum radius was fitted to the data for juveniles and adults (sexes combined and separate) and the equality of

Table 1

Catch data of *Galeorhinus galeus* during cruises conducted by the NOc *Atlantico Sul*. Asterisks indicate vertebrae collected.

Cruise code/year (month)	Sites	Latitudes (min.–max.)	Depth (m)	Male (n)	Female (n)
3/80 (June)	1	— —	120	19	370
4/80 (July)	1	— —	—	65	94
7/80 (Sep.)	7	30°44′–35°52′S	120	108	114
*7/81 (Sep.)	5	— —	—	55	161
9/81 (Sep.)	8	30°36′–34°24′S	120	184	276
3/82 (July)	10	— —	—	491	160
10/83 (Aug.)	7	30°42′–34°22′S	100	—	30
3/83 (Nov.)	14	30°44′–34°16′S	160	43	36
*4/84 (June)	15	— —	—	301	230
2/85 (June)	7	— —	—	72	104
*3/85 (July)	23	— —	—	76	101
*4/86 (July)	12	32°00′–34°00′S	500	65	414

Table 2

Sexual maturity of *Galeorhinus galeus* determined by size class. Data from Peres (1989).

	Total length (cm)	
	Males	Females
Juveniles	43–88	43–103
Adolescents	93–108	108–123
Adults	113–143	128–153

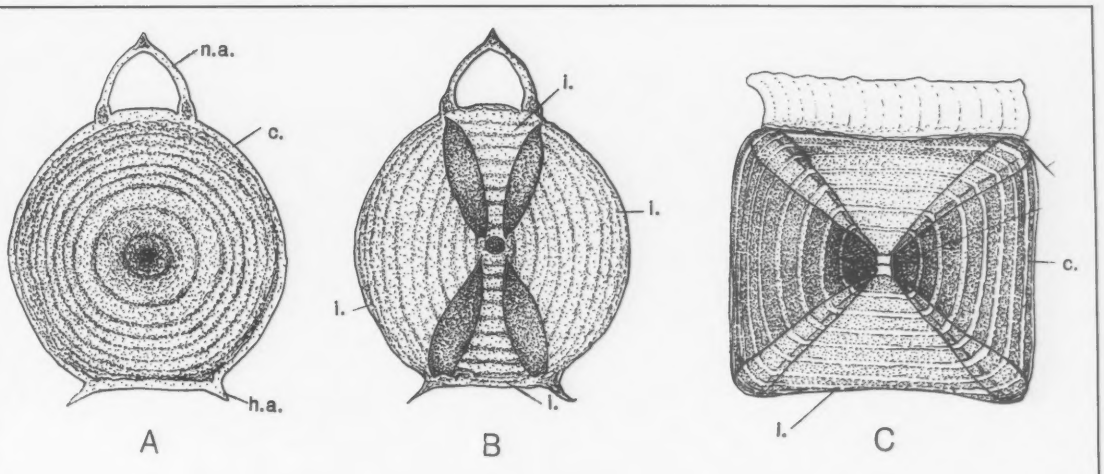


Figure 1

Drawings of *Galeorhinus galeus* vertebrae showing patterns of calcification in centra. (A) View from end of centrum toward focus, showing growth rings; (B) view at center of centrum, showing Maltese Cross of calcified radialia; (C) longitudinal view showing double cones and growth rings. c = centrum, h.a. = haemal arch, i = intermedialia, n.a. = neural arch.

slopes of the regression lines tested (Sokal and Rohlf 1981). As they were found to be different, a power relationship was fitted to TL × centrum radius for each sex. Each ring was measured and these values inserted into the power equation to back-calculate the length of each shark at formation of the respective ring. The von Bertalanffy growth model was fitted to the mean lengths-at-age, using the methods of Ford and Beverton as cited by Gulland (1977).

Results

Size composition

School sharks were present in the study area from April to November. During April and May all captured individuals were adolescent or adult gravid females (Fig. 2). From June to September the largest captures were registered (Table 1) and individuals from both sexes and all sizes (43–148 cm) were present (Figs. 2, 3). Larger juveniles were still captured during September, but individuals smaller than 70 cm TL were caught only from June to August.

A size variation within the sample size composition was also observed when analyzing the length frequencies plotted by cruise (Figs. 4, 5). Some size classes were better sampled during certain cruises. For instance, the sample was mainly composed of adults during cruises 3/80, 7/80, and 4/86, and of juveniles

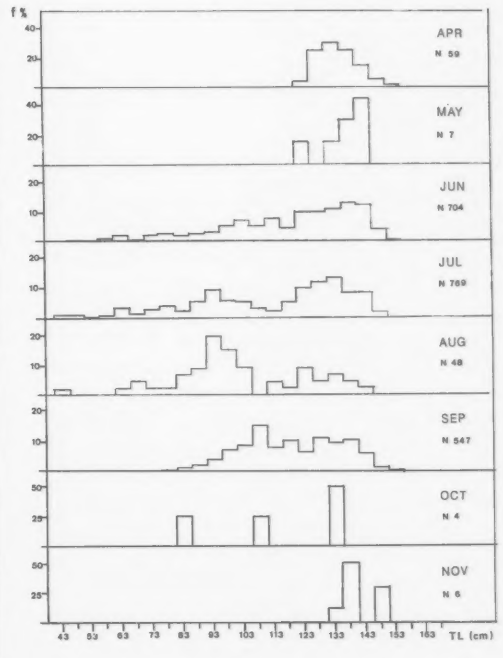


Figure 2

Length-frequency distribution of female *Galeorhinus galeus* by month.

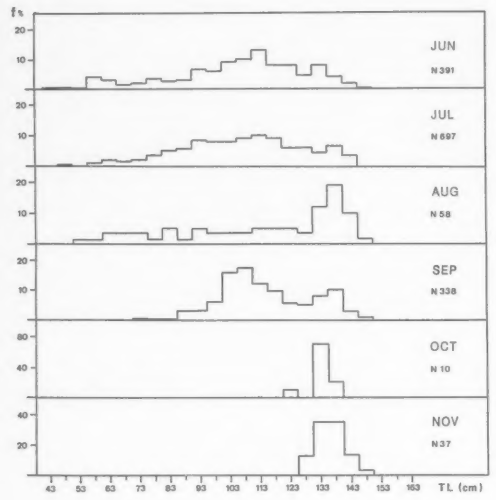


Figure 3
Length-frequency distribution of male *Galeorhinus galeus* by month.

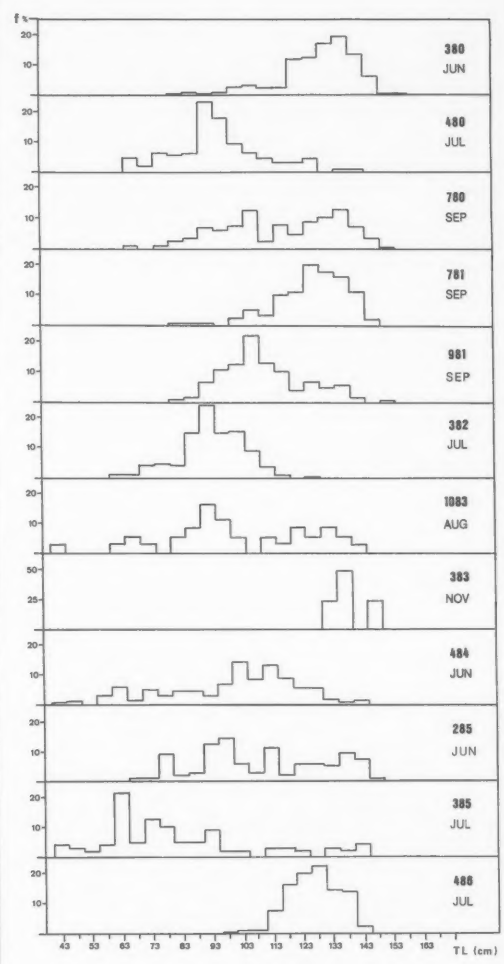


Figure 4
Length-frequency distribution of female *Galeorhinus galeus* by cruise.

during cruises 4/80, 9/81, and 3/82. Smaller length classes were more frequently caught during cruises 4/84 and 3/85, but did not form a marked mode in the length-frequency distribution.

Techniques for enhancing vertebral rings

Rings were visible in all the attempted methods, but because of the large number of rings and marginal crowding in the centra of older sharks, only detailed microscopic observations were successful in providing comprehensive readings and measurements. The graphite method was an easy and simple technique that provided good results in enhancing rings of vertebrae of younger sharks. However, the large number of rings near the margin of vertebrae of older sharks was difficult to determine using this technique, and the number of rings was always underestimated compared with results by other techniques.

Stained sections of vertebrae provided good results in enhancing rings both in calcified and decalcified material. In the latter, no measurements were taken because of shrinkage and distortions observed after the decalcification procedure. The matrix shrank in the space formerly occupied by the mineral, and this zone became narrower than in the calcified state.

The most satisfactory technique for enhancing and counting rings was microradiography. With this method, the more calcified zones appeared white while the less calcified appeared dark (Figs. 6, 8). Direct observations of the sections showed that the former more mineralized zones were translucent and the latter less-mineralized zones were opaque when observed under transmitted light (Figs. 7, 8). Sections of various thickness were examined. The best contrast between zones was obtained from sections between 250 and

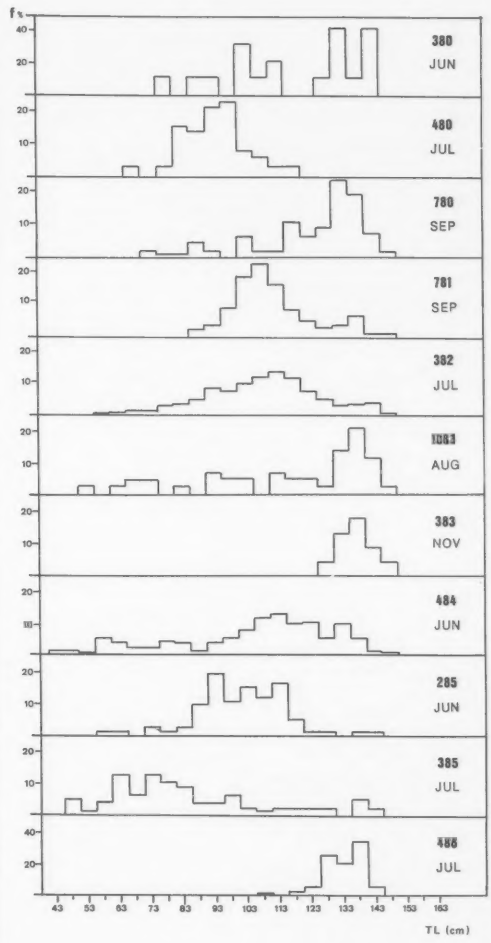


Figure 5
Length-frequency distribution of male *Galeorhinus galeus* by cruise.

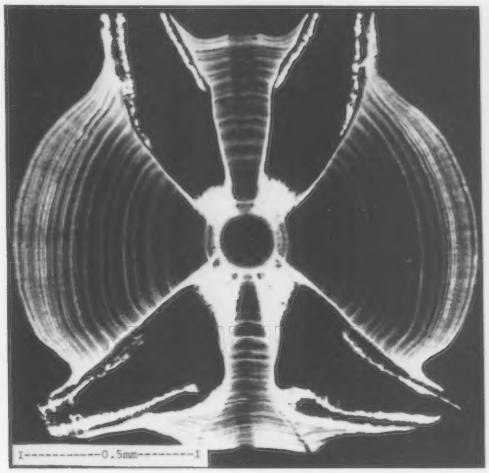


Figure 6
Microradiograph of transverse section of *Galeorhinus galeus* vertebra.

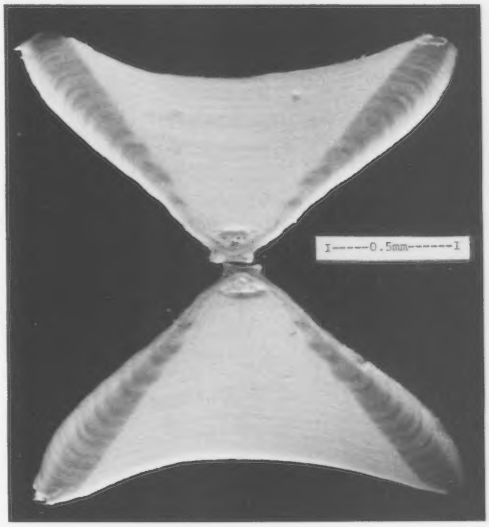


Figure 7
Sagittal section of *Galeorhinus galeus* vertebra under reflected light with dark background. Translucent zones appear dark and the opaque zones appear white.

750 μ for readings of interior rings and from 50 to 100 μ thick for readings on the margins.

Pattern of vertebral calcification

The vertebra of *Galeorhinus galeus* is composed of calcified cartilage. Its centrum consists of a corpus calcareum of two obtuse, hollow cones with their apices joined and opposed. The space around the two cones is organized into four oblique basalia and four calcified intermedialia: dorsal, ventral and lateral (Fig. 1) (Goodrich 1958, Ridewood 1921). In transverse section through the center of the centrum (focus), these radial

calcifications within the basalia have the shape of a Maltese Cross (White 1937) (Figs. 1B, 6). This "carcharinoid" pattern is characteristic of the families Triakidae, Sphyrnidae, and Carcharhinidae (Applegate 1967). Above the centrum is a neural arch. In the center of the centrum is a hole, marking the position of the primitive notochord, which we adopted as the focus of the vertebra. Within each cone, the focus is surrounded by a series of concentric rings which are read through techniques using the whole centra.

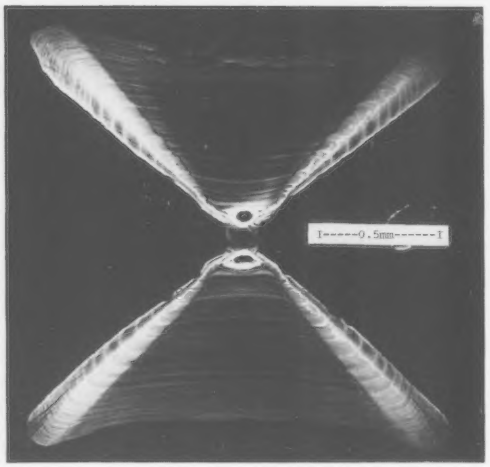


Figure 8
Microradiograph of sagittal section of *Galeorhinus galeus* vertebra from Figure 7. The more calcified zones (rings and cone in general) appear white, and the less calcified zones (opaque zones and intermedialia in general) appear dark.

The inside of each cone is lined by a perichondrium, which consists of a fibrous layer covering a germinative layer of chondroblast cells (Fig. 9). During growth phases, the chondroblasts differentiate into chondrocytes to form the mature cartilage, a densely cellular tissue consisting of rounded cells embedded in their secreted organic matrix. The body of the vertebra forming the intermedialia is also invested by a perichondrium. In sagittal section the differences between the two regions can be observed: the cells of the cone are smaller and embedded in a more abundant matrix than those of the intermedialia (Fig. 10). Mineralization occurs throughout the matrix and both regions present an alternate pattern of more and less mineralized zones, corresponding to the concentric rings that can be seen inside the cone.

The properties of the narrow and wide zones, which occur in an alternating sequence, were defined by comparing microradiographs and direct observations with transmitted and reflected light of sections of the same vertebra. In this species the narrow zone, which we define as a ring, is optically translucent and appears white on the radiograph, being opaque to the X-ray beam, and therefore more calcified. The wide zone, defined here as a growth zone, is optically opaque and appears dark on the radiograph, being semi-transparent to the X-ray beam, and therefore less calcified (Figs. 7, 8).

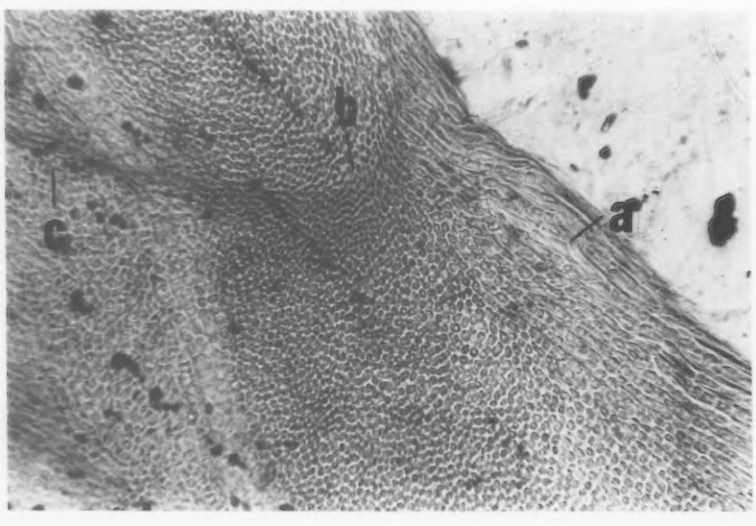


Figure 9
Sagittal section of *Galeorhinus galeus* vertebra showing part of the cone and intermedialia. Starting from external side: a = perichondrium; b = ring crossing cone; c = ring crossing intermedialia. (Harris's haematoxylin, 100×)

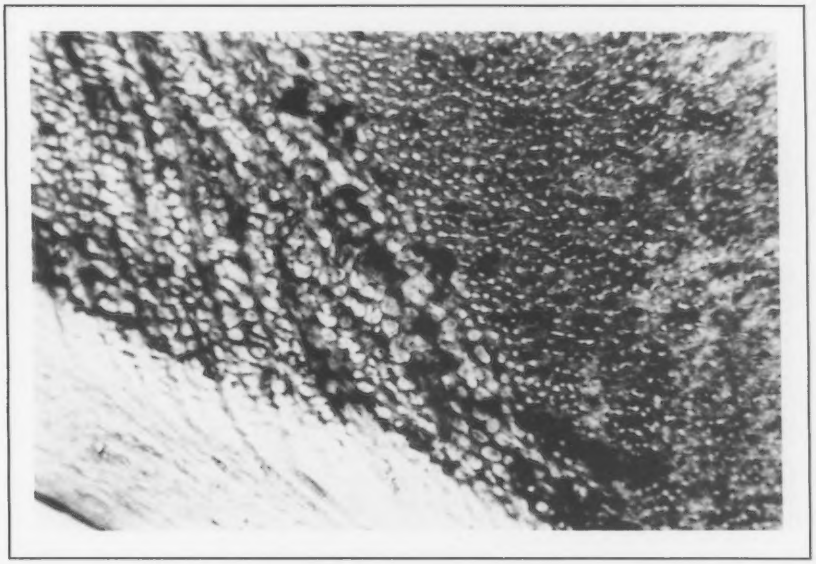


Figure 10
Sagittal section of *Galeorhinus galeus* vertebra showing contrasting tissue of cone and intermedialia. (Harris's haematoxylin, 100×)

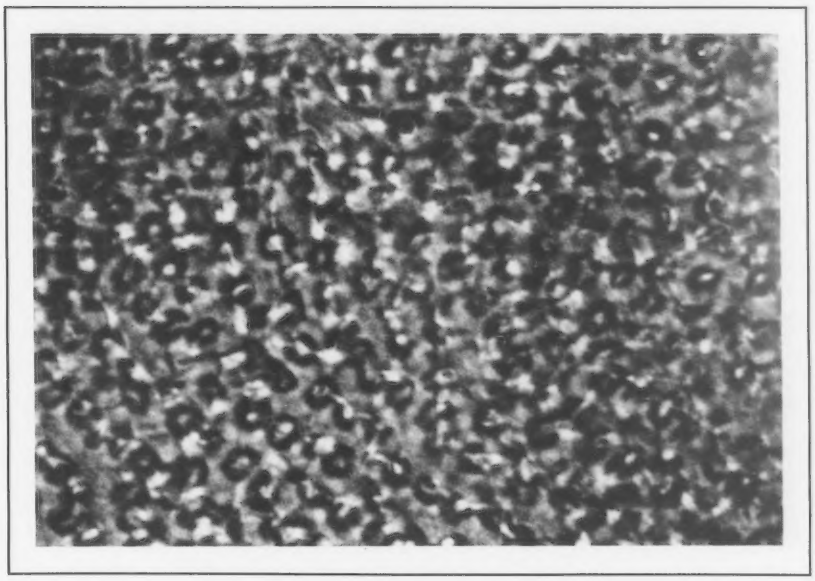


Figure 11
Section of vertebral tissue of *Galeorhinus galeus* showing the thin channels linking the cells. (Harris's haematoxylin, 400×)

Thin vascular channels connecting the cartilage cells were observed in haematoxylin-stained sections of resin-embedded vertebrae. These canaliculi form a network in the matrix between cells providing an opportunity for fluids and nutrients to reach the interior from the external medium (Fig. 11). Absence of lipid inclusions in the chondrocytes is interpreted as evidence of a healthy and active cellular metabolism. The presence of isogenic groups of cells suggests that cells divide interstitially and thus effect interstitial growth.

The widths of translucent and opaque zones varied in individuals. Rings were usually narrower than adjacent opaque zones, but with increased body size (TL), both attained the same average size (Figs. 12, 13). Width of a male's opaque zones decreases gradually, and after about the 15th ring the two zones are equal

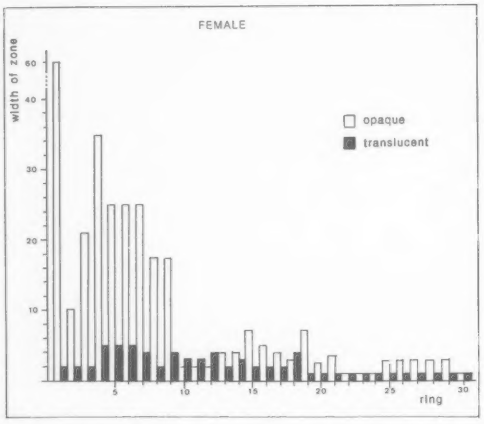


Figure 12
Widths (m.u. = 10^{-3} cm) of translucent and opaque zones distributed by ring for female *Galeorhinus galeus* (134 cm TL, 29 yrs-old).

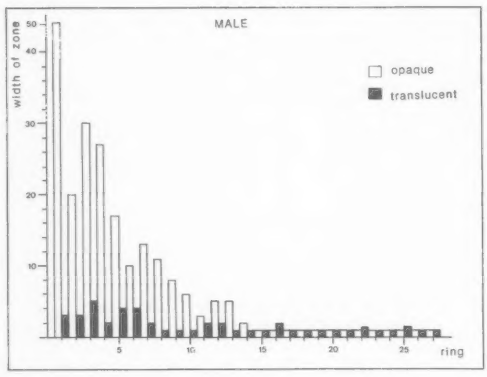


Figure 13
Widths (m.u. = 10^{-3} cm) of translucent and opaque zones distributed by ring for male *Galeorhinus galeus* (141 cm, 26 yrs-old).

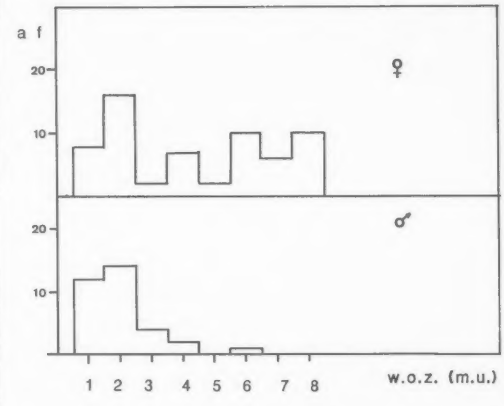


Figure 14
Frequency distribution of widths of opaque zones after the 15th ring for female and male *Galeorhinus galeus*.

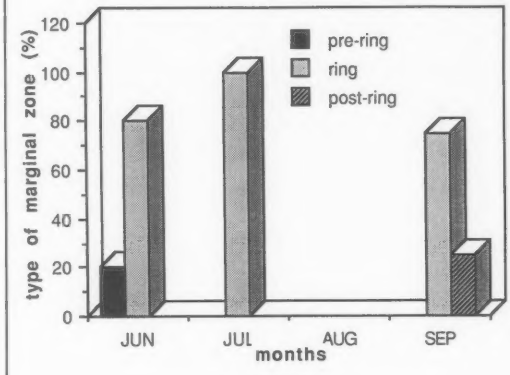


Figure 15
Percentage of type of marginal zone in vertebrae of *Galeorhinus galeus* observed June–September (n = 82).

in width. Females have the same general pattern, but some variation in width still can be detected after the 15th ring has been formed (Fig. 14).

From June to September, 91% of the vertebrae examined showed more calcified zones forming at the margins (Fig. 15). During June this percentage was 80%, rising to 100% during July and falling to 75% in September. The vertebrae observed with less calcified zones at margins during June (20%) were of the pre-ring type (wide less-calcified zone), and the ones observed during September (25%) were of the post-ring type (narrow less-calcified zone). These results indicated that the ring formation probably occurred during the winter months (June to September). One mark per year seems to be the most likely case for the school shark, and results here reflect this assumption.

In vertebrae of embryos at 8 months of intrauterine age, only the cartilage of cones was mineralized and no rings were visible (Fig. 16). Their intermedialia was

formed by a hyalin, unmineralized cartilage (Fig. 17). A 45 cm TL juvenile shark's vertebra showed some mineralization of the intermedialia, but unmineralized areas were still present. Two rings were observed (Fig. 18). The first ring was probably formed during the first winter after the birth in November (Peres 1989). The most recent one was just forming on the margin. In adult individuals the largest number of rings was 41, observed in a female of 155 cm TL.

Histological observations revealed the presence of a thin uncalcified layer at the very edge of the vertebrae, peripheral to the outermost narrow or wide calcified zones at the margin (Fig. 18). This indicates that the marginal growth of the vertebra starts with the formation of an unmineralized layer of cartilage which is subsequently mineralized. This layer is probably present throughout the year and does not by itself indicate periodicity of ring formation.

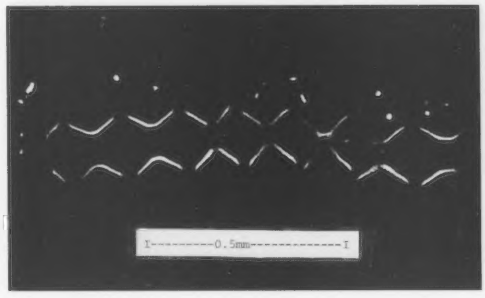


Figure 16
Microradiograph of a sagitally sectioned vertebral column from a *Galeorhinus galeus* embryo, showing calcification (white zones) of double cone in centrum (50×).

Back-calculation

All linear regressions of total length on vertebral radius were significant ($p<0.05$). The regression slopes were significantly different between juveniles and adults ($p<0.05$) and between adult males and females ($p<0.05$). Therefore, a power relationship was found to be more adequate to fit the pooled data for juveniles and adults of each sex. The following equations were obtained: Females ($N = 26$), $TL = 32.59 \times R^{0.827}$ and males ($N = 33$), $TL = 25.07 \times R^{0.897}$, where N indicates sample size and R radius of vertebra, with TL in cm and R in micrometric units (1 m.u. = 10^{-3} cm) (Fig. 19).

Lengths were back-calculated by age class and did not reveal the occurrence of Rosa Lee phenomenon (Gulland 1977), so the lengths at age were averaged (Table 3). The von Bertalanffy growth parameters were: females, $k = 0.075$, $L_\infty = 163$ cm, and $t_0 = -3.00$; males, $k = 0.092$, $L_\infty = 152$ cm, and $t_0 = -2.69$. The growth curves calculated from these parameters are shown in Fig. 20.

Using the ELEFAN software, several attempts were made to find the growth curve best fitted to the length-frequency data. In order to obtain a data set contain-

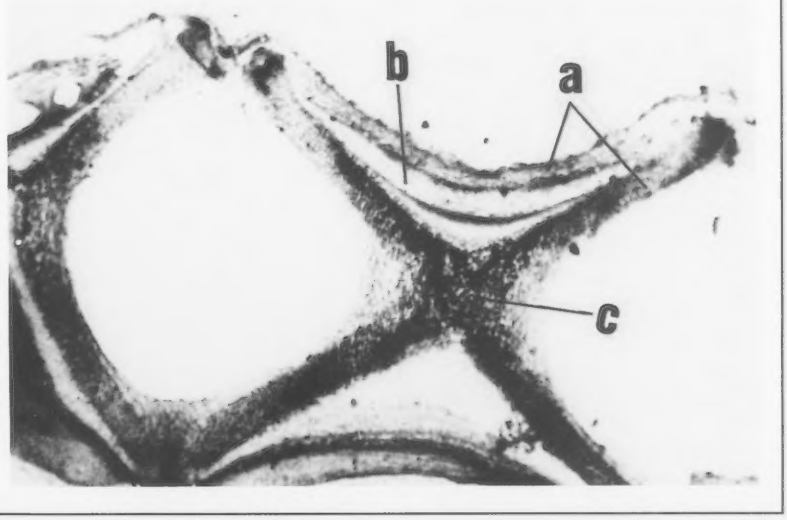


Figure 17
Sagittal section of vertebra from a *Galeorhinus galeus* embryo, showing (a) perichondrium, (b) hyaline cartilage in intermedialia, and (c) calcified cartilage of cones. (Haematoxylin, 100×)

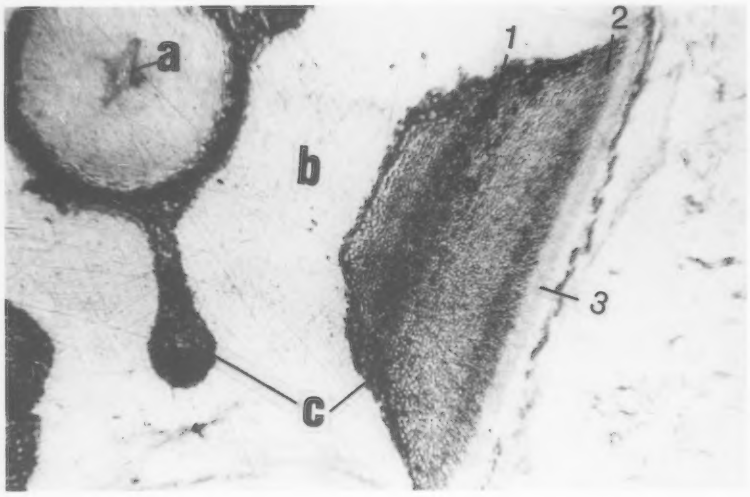


Figure 18
Portion of a transverse section of a vertebral centrum from a 2d-year *Galeorhinus galeus* juvenile, showing (a) focus, (b) hyaline cartilage, and (c) calcified cartilage of intermedialia. (1) 1st ring, (2) 2d ring, and (3) uncalcified margin. (Haematoxylin, 50×)

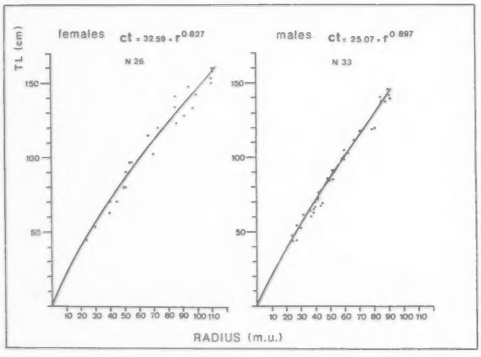


Figure 19
Relationship between total length and vertebra radius (R) for female and male *Galeorhinus galeus* (m.u. = 10^{-3} cm).

Table 3
Back-calculated lengths (TL, mm) at age for male and female *Galeorhinus galeus*.

Age (years)	Ring	Male (*n*)	Male TL	Female (*n*)	Female TL
0	1	18	343	18	323
1	2	17	464	18	424
2	3	16	545	17	496
3	4	16	616	15	579
4	5	12	693	13	668
5	6	12	762	11	747
6	7	8	818	10	818
7	8	5	893	9	890
8	9	4	947	9	946
9	10	4	998	9	992
10	11	4	1027	8	1037
11	12	4	1070	6	1048
12	13	3	1137	4	1091
13	14			4	1123
14	15			4	1152
15	16			2	1196
16	17			2	1215
17	18			1	1259
18	19			1	1309
19	20			1	1334
20	21			1	1347
21	22			1	1371

ing the widest possible range of TL at a given time of the year, the data for June and July 1985 were pooled. Von Bertalanffy growth parameters were obtained as follows: females, $k = 0.2$ and $L_\infty = 157$ cm (Rn = 612); and males, $k = 0.2$ and $L_\infty = 157$ cm (Rn = 429).

Discussion

The area of greatest uncertainty for interpreting and measuring growth zones in shark centra is near the margin (Casey et al. 1985). Distinguishing the presence of the last ring is a common problem (Casey et al. 1985, Stevens 1975, Walker 1986). Using microradiography, the margin can be easily observed in school shark

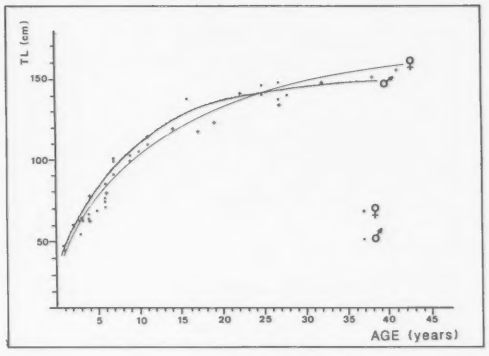


Figure 20
Von Bertalanffy growth curves for male and female *Galeorhinus galeus* and observed lengths-at-age.

vertebrae and the ring formation identified. This technique is not subject to problems derived from the presence of marginal connective tissue (Stevens 1975), and a large number of thin rings near the margin can be counted.

From observation of margins of vertebrae, we can conclude that ring formation probably occurred during the period June–September. The high percentages of ring formation observed in the sample indicated that the process probably extends over a larger period than observed in the current study, covering perhaps half of the year. The growth band would be formed during the remaining period, and the rings would thus be annual marks. However, as vertebrae were examined only for four-month periods (June–September), the need for a proper validation remains, as emphasized by Beamish and McFarlane (1983). The hypothesis that two rings could be formed during a year was disregarded, due mainly to the results of Grant et al. (1979). These authors estimated a longevity of 40 years for *Galeorhinus australis* (=*Galeorhinus galeus*, Compagno 1984) in South Australia, from mark-recapture data. Several individuals were recaptured after periods of more than 25 years at large, and 10% of the recaptures occurred 15 years after release. This evidence supported the hypothesis of one ring per year, which also led to the conclusion that individuals can attain up to 40 years of age.

Casey et al. (1985), observing a large number of rings near the margin, suggested that if these could be interpreted as annual marks, the ages determined for several species of sharks may have been underestimated. The present results agree with this hypothesis, and provide evidence that the school shark is a long-lived, slow-growing species.

The conclusion that the rings are translucent and strongly calcified, while the growth bands are optically opaque and less calcified is in agreement with the fact that the rings are stained dark by the silver nitrate technique (Stevens 1975, Cailliet et al. 1983). Casselman (1974, 1983) concluded that the translucent zone in calcified tissue of fish is more heavily mineralized than adjacent opaque zones and that calcium content is directly related to translucency.

In reference to the mode of calcification of cartilage, Moss (1977) wrote that "something radically different occurs in shark cartilage, making it certain that there can be no unitary description of vertebrate cartilaginous calcification." Hoenig and Walsh (1982) described the occurrence of vascularized cartilage canals in calcified vertebrae of several species of sharks. Many canals were found to contain blood cells, and they suggested a nutritive role for these canals. However, diffusion through the matrix is impossible after mineralization and in mammals; for instance, calcification of endochondral bone causes cellular degeneration and death of chondrocytes, because the isolated cells cannot maintain a normal metabolism (Robbins 1975). In the school shark, however, chondrocytes remain alive after calcification, as is evident from their normal, lipid-free appearance in calcified zones. Interchange between cells and vascular elements is probably sustained after mineralization by the canaliculi that were observed permeating the intercellular matrix.

The growth of crystals within a preformed organic structure is the basic mode of skeletal formation (Weiner 1984). Narrow uncalcified matrix areas observed at the edge of school shark vertebrae show that development of hyaline cartilage precedes the process of calcification. In addition, evidence of interstitial growth indicates that the tissue still remains uncalcified for a while after the appositional growth. In the vertebrae of embryos only the cone area was calcified. Among juveniles some uncalcified zones occurred also in the intermedialia. During the adult phase, the cone and intermedialia display the same mineralization pattern, with corresponding opaque and translucent alternate zones. This is evidence that the calcification, even when occurring at different times, follows the same pre-established rules. Weiner (1984) suggests that the organic matrix performs active, specific roles in this process. Growth of hydroxyapatite crystallites occurs in the space between collagen fibrils and perhaps within them (Glimcher *in* Kemp 1984). Therefore, regions of organic matrix formed during slow-growth phases would offer more space for crystal growth when exposed to the calcium and phosphate ions which form the mineral crystallites. Such regions, e.g., the rings,

would be characterized by relatively heavier calcification compared with the more rapidly growing, less calcified zones. In addition, the formation of the ring takes at least 4 months, but during the first 10 years of life the width of a ring is much less, in comparison with adjacent growth bands, than it would be if the growth rate were constant throughout the year. It is concluded that in *G. galeus* the ring represents a period of slow growth, and that mineralization is more intense during this period.

Vooren and Betito (In press) have shown that individuals of *Galeorhinus galeus* migrate northwards into the study area starting in April, until their peak abundance in September. At this time the school shark is abundant on the shelf south of lat. 32°S and scarce or absent further north. After September, the fish migrate southward from the study area, are scarce there in November, and absent in January and February. At the onset of winter, a marked change in temperature preference occurs, with most fishes occurring at 18–20°C from April to June and at 11–15°C in August and September, although water masses of higher temperatures are available during the latter months. The present data show that gravid females arrive first, making up all the April and May catches. From June onwards, other groups (adult males, non-gravid adult females and juveniles of both sexes) migrate into the area. The whole population experiences the decrease in temperature from June to August (Vooren and Betito In press). Thus, the period of slow growth and ring formation in vertebral centra coincides with this change in temperature preference of the population at the onset of winter. Similar results have been reported for other species (Stevens 1975, Jones and Geen 1977), confirming the general view that ring formation is associated with low temperature and slow vertebral growth (Longhurst and Pauly 1987).

As for the process involved, Casselman (1974) has suggested that during slow-growth phases, the amount of protein available for appositional growth might be reduced although minerals would still be available. In the shark vertebra, slow growth is evidently associated with a reduced rate of deposition of matrix components, which include both collagen fibrils and polysaccharides. Digestion and depletion of the carbohydrate moiety of the matrix during the slow-growth phase would facilitate interaction between collagen fibrils and mineral ions, thus promoting calcification. Mugiya (1987) has shown that in fish otoliths both calcium uptake and protein synthesis vary in an endogenous process controlled by hormones. In the school shark vertebrae, a matrix less dense in protein formed during slow-growth phases could be the cue to a higher calcium uptake to fill the space available for mineralization. Jones and Geen (1974) related wider rings with warmer years in spines of *Squalus acanthias*, and this relationship may explain the variation in the width of the rings which is observed in vertebrae of adult female school sharks (Fig. 15). Gravid females which migrate into the study area during March to May show preference for higher temperatures, and it is possible that they remain in the warmer part of the species' temperature range during the winter. If so, their rings might grow faster than in fishes that remain at lower temperatures. The distribution of the different components of the population in the study area during the winter should be investigated in detail to test this hypothesis.

Reading vertebrae is the most important tool for age determination in many elasmobranchs. Length-frequency analysis is most suitable for fast-growing species because of the assumption that all fishes in the sample have the same age at the same length (Longhurst and Pauly 1987). In slow-growing, long-lived species, however, a given size class contains several different age groups (Gruber and Stout 1983). The Von Bertalanffy growth parameters estimated by ELEFAN software (Pauly and David 1981), using length-frequency data, overestimated the growth rate determined by vertebral readings. These values were approximately the same as those found by Olsen (1954) when analyzing length-frequency data for the Australian school shark. Later, Grant et al. (1979), using tag-recapture methods, estimated lower values of growth rates and concluded that length-frequency analysis was impracticable in this species.

Acknowledgments

Special thanks are due to Dr. Daoiz Mendoza for all his help and assistance with the histological aspects of this work. We thank Monica B. Peres for the valuable information and Mauro Maida, Dr. Garry R. Russ, Marcus V.S. Ferreira, and Annadel Cabanban for their constructive criticisms of the manuscript. We also thank the people from Projeto Talude and RV *Atlantico Sul* who helped with the field work. The research was sponsored by the Brazilian Ministry of Science and Technology (CNPq).

Citations

Applegate, S.P.
1967 A survey of shark hard parts. *In* Gilbert, P.W., R.F. Mathewson, and D.P. Rall (eds.), Sharks, skates and rays, p. 37–67. John Hopkins Press, Baltimore.

Beamish, R.J., and G.A. McFarlane
1983 The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743.

Cailliet, G.M., L.K. Martin, D. Kusher, P. Wolf, and B.A. Welden
1983 Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. *In* Proceedings of the international workshop on age determination of oceanic pelagic fishes: Tunas, billfishes and sharks, p. 157–165. NOAA Tech. Rep. NMFS 8.

Casey, J.G., H.L. Pratt Jr., and C.E. Stillwell
1985 Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the Western North Atlantic. Can. J. Fish. Aquat. Sci. 42:963–975.

Casselman, J.M.
1974 Analysis of hard tissue of pike *Esox lucius* L. with special reference to age and growth. *In* Bagenal, T.B. (ed.), Ageing of fish, p. 13–27. Unwin Bros., Surrey, England.
1983 Age and growth assessment of fishes from their calcified structures — Techniques and tools. *In* Proceedings of international workshop on age determination of oceanic pelagic fishes: Tunas, billfishes and sharks, p. 1–17. NOAA Tech. Rep. NMSF 8.

Compagno, L.J.V.
1984 Sharks of the world. FAO species catalogue. FAO Fish. Synop. 4 (125), pt. 2:386–389.

Goodrich, E.S.
1958 Studies on the structure and development of vertebrates, Vol I. Dover Publ. Inc., NY, 485 p.

Grant, C.J., R.L. Sandland, and A.M. Olsen
1979 Estimation of growth, mortality and yield per recruit of the Australian school shark, *Galeorhinus australis*, from tag recoveries. Aust. J. Mar. Freshwater Res. 30:625–637.

Gruber, S.H., and R.G. Stout
1983 Biological materials for the study of age and growth in a tropical marine elasmobranch the lemon shark, *Negaprion brevirostris* (Poey). *In* Proceedings of the international workshop on age determination of oceanic pelagic fishes: Tunas, billfishes and sharks, p. 193–205. NOAA Tech. Rep. NMFS 8.

Gulland, J.A. (editor)
1977 Fish population dynamics. John Wiley, NY, 372 p.

Hoenig, J.M., and A.H. Walsh
1982 The occurrence of cartilage canals in shark vertebrae. Can. J. Zool. 62:483–485.

Jones, B.C., and G.H. Geen
1977 Age determination of an elasmobranch (*Squalus acanthias*) by X-ray spectometry. J. Fish. Res. Board Can. 34:44–48.

Kemp, N.E.
1984. Organic matrices and mineral crystallites in vertebrate scales, teeth and skeletons. Am. Zool. 24:965–976.

Longhurst, A.R., and D. Pauly
1987 Ecology of tropical oceans. Acad. Press, San Diego, 407 p.

Moss, M.L.
1977 Skeletal tissue in sharks. Am. Zool. 17:335–342.

Mugiya, Y.
1987 Phase difference between calcification and organic matrix formation in the diurnal growth of otoliths in the rainbow trout *Salmo gairdneri*. Fish. Bull., U.S. 85:395–401.

Nie, N.H., C.H. Hull, J.C. Jenkins, K. Steinbrenner, and D.H. Bent
1975 Statistical package for the social sciences, 2d ed. MacGraw-Hill, Boston, 675 p.

Olsen, A.M.
1954 The biology, migration and growth rate of the school shark, *Galeorhinus australis* (MacLeay) in south-eastern Australian waters. Aust. J. Mar. Freshwater Res. 5:353–410.

Pauly, D., and N. David
1980 An objective method for determining fish growth from length-frequency data. ICLARM (Int. Cent. Living Aquat. Resourc. Manage.) Contrib., Newsl. 3(3):13–15.
1981 ELEFAN 1, a BASIC program for the objective extraction of growth parameters from length frequency data. Meeresforschung/Rep. Mar. Res. 28(4):205–211.

Peres, M.B.
1989 Desenvolvimento, ciclo reprodutivo e fecundidade do cacao bico-de-cristal *Galeorhinus galeus* L. no Rio Grande do Sul. MSc. thesis, Fundacao Universidade do Rio Grande, RS, Brasil, 76 p. [in Portuguese, Engl. abstr.].

Ridewood, W.G.
1921 On the calcification of the vertebral centra in sharks and rays. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 210:311–407.

Robbins, S.L.
1975 Patologia estructural e funcional. Interamericana, Mexico, 1516 p.

Sokal, R.R., and F.J. Rohlf
1981 Biometry, 2d ed. W.H. Freeman, NY, 859 p.

Stevens, J.D.
1975 Vertebral rings as a means of age determination in the blue shark *Prionace glauca*. J. Mar. Biol. Assoc. U.K. 55: 657–665.

Vooren, C.M., and R. Betito
In press. Distribution and abundance of demersal elasmobranch fishes on the continental shelf of Rio Grande dc Sul, Brazil. Bull. Mar. Sci.

Walker, T.I.
1986 Southern shark assessment project. 2d Review, October 1986. Mar. Sci. Lab. Prog. Rev. 66, Queenscliff, Victoria, Australia, 48 p.

Weiner, S.
1984 Organization of organic matrix components in mineralized tissues. Am. Zool. 24:945–951.

White, E.G.
1937 Interrelationships of the elasmobranchs with a key to the order Galea. Bull. Am. Mus. Nat. Hist. 74:25–138.

Chaetognatha from the Central and Southern Middle Atlantic Bight: Species Composition, Temperature-Salinity Relationships, and Interspecific Associations*

George C. Grant

Virginia Institute of Marine Science and School of Marine Science
The College of William and Mary, Gloucester Point, Virginia 23062

Abstract.– Eighteen species of chaetognaths were identified from shelf waters in the Middle Atlantic Bight. Species composition in the water column and the hyponeuston was nearly identical, but the percent frequencies of the more common cold-temperate species were generally lower in surface collections. Mean surface salinity, weighted for abundance of individual chaetognath species in the hyponeuston collections, varied from 32.6 and 32.8 ‰ for the coastal- and estuarine-inhabiting *Sagitta tenuis* and *Parasagitta elegans*, to 34.8 and 34.9 for the offshore *Pterosagitta draco* and *Krohnitta pacifica*. Weighted mean temperatures ranged from below 14°C for *Mesosagitta minima*, *P. elegans*, and *Serratosagitta tasmanica* to over 24°C for *K. pacifica*. Overall association among Middle Atlantic Bight chaetognaths, measured for the 15 most frequent species in 716 collections by variance ratio, was significantly positive. Association between pairs of species was therefore also largely positive, with the important exception of *Parasagitta elegans*. This species, with a unique regional niche in low salinities and temperatures, was negatively associated ($p<0.01$) with five warm-water species (*Krohnitta pacifica*, *Ferosagitta hispida*, *Sagitta tenuis*, *Sagitta helenae*, and *Flaccisagitta enflata*). Most species reached maximum abundance at the surface near midnight. Exceptions included *Sagitta helenae*, with daylight maxima, and *Krohnitta pacifica*, *Ferosagitta hispida* and *Serratosagitta serratodentata*, showing crepuscular increases in abundance.

Manuscript accepted 12 October 1990.
Fishery Bulletin, U.S. 89:33–40 (1991).

Recognition of several chaetognath species along the northeastern coast of the United States is quite recent. Until 1960, only eight species had been identified from shelf waters off the Middle Atlantic states, i.e., the Middle Atlantic Bight from Cape Cod to Cape Hatteras; these were included in Bigelow and Sears (1939): *Eukrohnia hamata*, *Parasagitta elegans*, *Flaccisagitta enflata*, *Serratosagitta serratodentata* (including the then undescribed *Serratosagitta tasmanica*), *Flaccisagitta hexaptera*, *Pseudosagitta maxima*, *Krohnitta subtilis*, and *Pterosagitta draco***. Deevey (1960), in a study of the Delaware Bay region, added *Ferosagitta hispida*, *Sagitta helenae*, and *Mesosagitta minima* to the list of recognized species. Since her material had been collected three decades earlier (1929–31), it appears that pre-1960 studies had simply failed to distinguish between grossly similar species. *Sagitta tenuis*, *Sagitta bipunctata*, and *Krohnitta pacifica* were added by Grant (1963a, b) to the list of shelf species, and Grant (1967) later confirmed that the endemic shelf population of "*S. serratodentata*" in this region was actually *S. tasmanica*. Grice and Hart (1962) found other species in slope waters southeast of Long Island, New York, including *Pseudosagitta lyra*, *Mesosagitta decipiens*, and *Solidosagitta planctonis*. Thus, at the close of the 1960s, some 15 species were known from the shelf and the presence of others in surface slope waters suggested their likely occurrence over the shelf as well.

This study of Middle Atlantic Bight chaetognaths is based on an intensive series of collections from the central and southern bight. Presented here are the species composition in hyponeuston and subsurface collections, temperature-salinity-plankton (T-S-P) diagrams for the more common surface species, measurements of interspecific associations among chaetognaths, and a summary of diel abundance in the hyponeuston.

Methods and materials

Chaetognath collections

A transect of six stations (C1-J1, Fig. 1) off southern New Jersey was sampled quarterly for two years, October 1975–August 1977. Two more northerly stations (A2, B5) and a southern transect of four stations (L1-L6) were added in the second survey year

* Contribution No. 1624 from the Virginia Institute of Marine Science and School of Marine Science, The College of William and Mary.

** Taxonomy in this paper generally follows the revisions of Tokioka (1965) and Kassatkina (1971), but removes *Pseudosagitta lyra* and *P. maxima* from the genus *Flaccisagitta* in agreement with species groupings of Alvariño (1963).

(Grant 1977a, 1979, 1988). Routine collections at each station included paired 60-cm bongo net samplers (202 and 505 μm mesh nets), towed from just below the surface to near, but safely off, the bottom, then back to the surface (so-called double oblique tows; 220 samples), and eight surface layer (upper 10 cm) collections obtained at 3-hour intervals over a 24-hour period (496 samples), using a 1-m wide hyponeuston net (505 μm mesh). Of the 716 collections (Table 1), only 1 bongo and 79 hyponeuston (mostly daytime) collections lacked chaetognaths.

Laboratory processing

Collections were divided into successively smaller aliquots for the more numerous taxa, using a sample-splitting device of proven design (Burrell et al. 1974). However, chaetognaths were generally obtained from whole or half samples, unless very abundant.

Data analysis

Collection data were sorted by species, stations, and collection methods. Analysis of the relationship of species abundance to hydrography was limited to hyponeuston collections because subsurface tows were oblique, often traversing multiple layers of different water types. Mean temperatures and salinities of capture in surface-layer collections were calculated for each common chaetognath species, weighting each observed temperature and salinity by the size of catch ($\log N + 1$), where N = total catch in a standard 20-minute hyponeuston net tow at 2.5 knots. Thus,

$$\bar{T} = \frac{t_1(\log n_1 + 1) + t_2(\log n_2 + 1) + \ldots + t_n(\log n_n + 1)}{(\log n_1 + 1) + (\log n_2 + 1) + \ldots + (\log n_n + 1)}$$

$$\bar{S} = \frac{s_1(\log n_1 + 1) + s_2(\log n_2 + 1) + \ldots + s_n(\log n_n + 1)}{(\log n_1 + 1) + (\log n_2 + 1) + \ldots + (\log n_n + 1)}$$

where t_i, s_i, and n_i are the surface temperature, surface salinity, and total catch in each positive collection, respectively.

Presence, absence, and joint occurrences of the 15 most frequent species from both bongo and hyponeuston collections were used in an analysis of association between and among species. As recommended by Ludwig and Reynolds (1988), the significance of association among all 15 species and 716 collections was first tested simultaneously using a variance ratio (VR) derived from a null association model (Schluter 1984). The expected value of VR under the null hypothesis of independence is 1. When VR>1, a positive association of species is indicated; VR<1 indicates a negative association. A test statistic W = (N)(VR) provides a test of significance for deviations from 1. If species are not associated there is a 90% probability that W lies between the chi-square limits:

$$\chi^2_{0.05,N} < W < \chi^2_{0.95,N}.$$

Because of the large degrees of freedom in this study (where N = 716), critical values of χ^2 were approximated (see Zar 1984, p. 482).

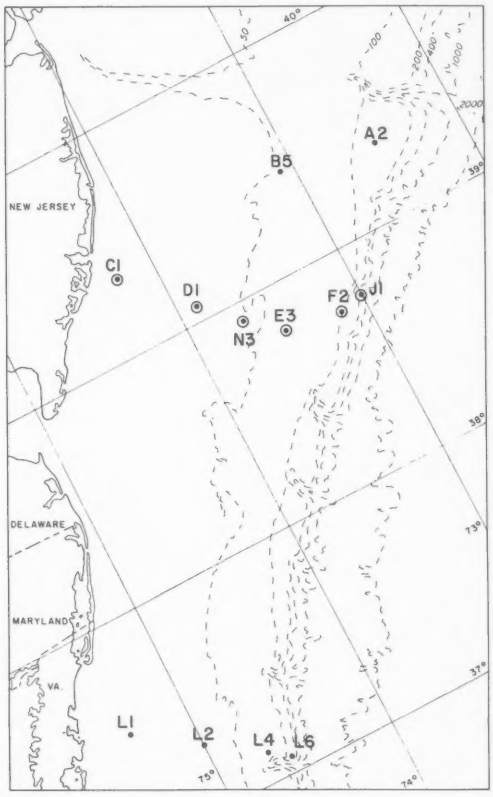


Figure 1
Location of Middle Atlantic Bight plankton stations (●) sampled quarterly, October 1975–August 1977. Those in transect off New Jersey (C1–J1, ⊙) were sampled for 2 years. Other stations were added for the second year. Depth contours in meters.

Relative strength of the association between pairs of species was measured using 2×2 contingency tables and Hurlbert's (1969) coefficient of interspecific association (C_8), as corrected by Ratliff (1982) for errors resulting from lack of absolute association (Pielou 1977). Yates' correction of chi-squared calculations was applied for low expected frequencies (Bailey 1981).

Table 1
Number of zooplankton collections obtained during eight seasonal cruises in the Middle Atlantic Bight, 1975–77.

		Subsurface		Surface	
		60-cm bongo nets		1-m hyponeuston net	
Cruise	Dates	202 μm	505 μm	505 μm	Total
1	23–29 Oct 75	6	6	48	60
2	5–16 Feb 76	6	6	48	60
3	8–16 Jun 76	6	8	52	66
4	31 Aug–9 Sep 76	6	7	48	61
5	5–28 Nov 76	22	21	75	118
6	20 Feb–6 Mar 77	21	21	75	117
7	17–28 May 77	21	21	75	117
8	19–29 Aug 77	21	21	75	117
Total		109	111	496	716

Results

Species composition

Eighteen species (11 genera) of chaetognaths were identified, 17 in both surface hyponeuston and subsurface bongo net collections (Tables 2 and 3). Compositional differences in the two lists were limited to the rarest species: *Sagitta bipunctata* was found only in hyponeuston collections, while *Pseudosagitta maxima* was restricted to subsurface collections. After adjustment for the 80 collections devoid of chaetognaths (79 surface and 1 subsurface collections), the percent frequencies of the most common cold-temperate species (*Serratosagitta tasmanica*, *Parasagitta elegans*, and *Mesosagitta minima*) were found to be much lower in surface collections. Warm-water chaetognaths (*Flaccisagitta enflata*, *Sagitta helenae*, *Pterosagitta draco*, *S. tenuis*, *Serratosagitta serratodentata*, *Ferosagitta hispida*, and *Krohnitta pacifica*) were either equally frequent in the two types of collections or more frequent in the hyponeuston.

Table 2
Percent frequency of chaetognath species occurrence in hyponeuston collections from eight quarterly cruises, 1975–77.

Cruise:	1	2	3	4	5	6	7	8	Total
Number of collections:	48	48	52	48	75	75	75	75	496
Serratosagitta tasmanica	50.0	43.8	48.1	33.3	66.7	61.3	17.3	21.3	42.5
Flaccisagitta enflata	18.8	—	1.9	81.2	77.3	34.7	24.0	73.3	41.9
Parasagitta elegans	35.4	85.4	92.3	14.6	6.7	16.0	58.7	14.7	37.3
Mesosagitta minima	2.1	22.9	—	—	50.7	30.7	2.7	9.3	16.5
Sagitta helenae	4.2	—	—	8.3	24.0	18.7	20.0	8.0	11.9
Ferosagitta hispida	—	—	—	35.4	21.3	—	1.3	14.7	9.1
Pterosagitta draco	2.1	8.3	—	16.7	8.0	17.3	6.7	—	7.5
Sagitta tenuis	—	—	—	31.2	20.0	—	1.3	2.7	6.7
Krohnitta pacifica	—	—	—	—	—	—	9.3	24.0	5.0
Serratosagitta serratodentata	—	—	—	4.2	4.0	6.7	2.7	8.0	3.6
Flaccisagitta hexaptera	—	10.4	—	10.4	2.7	6.7	—	—	3.4
Krohnitta subtilis	—	—	—	4.2	1.3	2.7	1.3	1.3	1.2
Mesosagitta decipiens	—	—	—	2.1	—	6.7	—	—	1.2
Pseudosagitta lyra	—	2.1	—	—	—	4.0	—	—	0.8
Eukrohnia hamata	—	2.1	—	—	—	2.7	—	—	0.6
Sagitta bipunctata	2.1	—	—	—	—	—	1.3	—	0.4
Solidosagitta planctonis	—	—	—	—	—	—	1.3	—	0.2

Temperature-salinity-abundance relationships

The chaetognaths were collected in a wide range of temperatures (2.2–26.6°C) and salinities 27.7–36.0‰ (Table 4). Weighted means of surface salinities measured at the time of hyponeuston collections were very similar among all common surface species, ranging from 32.6 and 32.8‰ for *Sagitta tenuis* and *Parasagitta elegans*, respectively, to 34.9‰ for *Krohnitta pacifica* (Table 4). Weighted mean temperatures, on the other hand, varied widely among species, from 12.9°C for *Mesosagitta minima* to 24.2°C for *K. pacifica*. Species occurring infrequently at the surface and excluded from Table 4 were those residing at greater depths, with surface occurrences mostly restricted to low winter temperatures. Relationships between surface abundance of common species and the two physical factors were further examined by plotting average daily catch (8 collections at 3-hour intervals) in standard hyponeuston collections, defined previously (Grant 1988) as 1-m neuston nets towed at 2.5 knots for 20 minutes; the sampler used typically fished the upper

10 cm of the sea surface so would more accurately be called a 'hyponeuston' net. Temperatures and salinities measured during collections containing chaetognaths were averaged at each positive station (Figs. 2 and 3).

Flaccisagitta enflata, *Sagitta tenuis*, *Ferosagitta hispida*, and, to a lesser extent, *S. helenae* and *Pterosagitta draco* were absent or uncommon in temperatures less than about 9°C (Figs. 2, 3), while few *Parasagitta elegans*, *Mesosagitta minima*, and *Pterosagitta draco* were found in warmest temperatures. *Serratosagitta tasmanica* was present in a very wide range of both temperature and salinity. Numbers of *Pterosagitta draco* were reduced in lower salinities as well as low temperatures; occurrences were in salinities higher than 34‰ except in the summer of 1976. *Sagitta helenae* and *Mesosagitta minima* were more frequent and numerous in higher salinities, while *S. tenuis* was absent from salinities greater than 35‰. Other species in Figures 2 and 3 were captured in various salinities.

Table 3

Percent frequency of chaetognath species occurrence in subsurface bongo collections from eight quarterly cruises, 1975–77.

Cruise:	1	2	3	4	5	6	7	8	Total
Number of collections:	12	12	14	13	43	42	42	42	220
Serratosagitta tasmanica	100.0	75.0	78.6	84.6	95.3	95.2	21.4	85.7	77.3
Parasagitta elegans	91.7	91.7	100.0	61.5	25.6	52.4	98.6	90.5	70.9
Flaccisagitta enflata	33.3	8.3	–	76.9	72.1	50.0	14.3	92.9	50.9
Mesosagitta minima	8.3	33.3	7.1	30.8	65.1	69.0	14.3	64.3	45.4
Sagitta helenae	–	–	–	–	18.6	26.2	14.3	9.5	13.2
Eukrohnia hamata	–	8.3	14.3	15.4	16.3	23.8	9.5	2.4	12.3
Flaccisagitta hexaptera	16.7	33.3	14.3	30.8	11.6	7.1	2.4	2.4	10.0
Pterosagitta draco	–	–	7.1	15.4	7.0	14.3	9.5	2.4	7.7
Sagitta tenuis	–	–	–	38.5	11.6	2.4	–	4.8	5.9
Serratosagitta serratodentata	–	–	–	–	2.3	2.4	4.8	16.7	5.0
Pseudosagitta lyra	–	8.3	–	–	4.7	7.1	7.1	2.4	4.5
Krohnitta subtilis	–	–	–	–	–	14.3	–	7.1	4.1
Ferosagitta hispida	–	–	–	23.1	7.0	–	–	4.8	3.6
Krohnitta pacifica	–	–	–	–	–	–	2.4	11.9	2.7
Mesosagitta decipiens	–	–	–	–	2.3	9.5	–	2.4	2.7
Solidosagitta planctonis	–	–	–	–	–	4.8	–	–	0.9
Pseudosagitta maxima	–	–	7.1	–	–	2.4	–	–	0.9

Table 4

Weighted means and ranges of temperature and salinity from surface collections at capture of the more frequent hyponeustonic chaetognaths, all cruises combined.

Species	Number of collections	Temperature (°C)		Salinity (‰)	
		$\bar{T}$	Range	$\bar{S}$	Range
Krohnitta pacifica	25	24.24	17.0–26.6	34.89	31.6–36.0
Serratosagitta serratodentata	18	21.25	8.1–26.6	34.57	31.7–35.9
Ferosagitta hispida	45	20.15	9.4–25.9	33.56	31.7–35.7
Flaccisagitta enflata	209	18.57	8.1–26.6	33.68	31.5–36.0
Sagitta helenae	58	16.76	6.3–26.6	34.38	31.7–36.0
Pterosagitta draco	37	15.87	8.1–22.3	34.75	32.4–35.9
Sagitta tenuis	33	15.83	9.1–24.6	32.59	31.7–34.8
Flaccisagitta hexaptera	17	14.00	8.4–22.3	34.56	33.1–35.8
Serratosagitta tasmanica	211	13.46	2.3–25.9	33.72	30.5–36.0
Parasagitta elegans	186	13.39	2.2–24.1	32.82	27.7–35.8
Mesosagitta minima	82	12.94	4.4–24.3	34.42	31.8–35.9

Interspecific association

Before examining association between pairs of species, the data were first tested for overall association using a matrix of the presence or absence of the 15 most common chaetognaths in 716 collections. Schluter's (1984) index of overall association (VR here, as in Ludwig and Reynolds 1988) for these 15 species was 2.108, indicative of a net positive association among the species. The null hypothesis of no association was rejected ($W = 1509$; 90% probability $654.9 < W < 779.3$).

Among paired-species associations, most statistically significant coefficients ($P < 0.05$) were positive (Table 5). Significant negative associations ($C_8 = -0.15$ to -0.73) were limited to six pairings of various species with *Parasagitta elegans* and the pair *Sagitta tenuis*–*Mesosagitta minima*. The sole significant positive association of *P. elegans* ($P < 0.05$) was with *Serratosagitta tasmanica*. Highest positive coefficients included associations among (1) the other most frequent chaetognaths, *Serratosagitta tasmanica*, *Mesosagitta minima*, and *Flaccisagitta enflata* ($C_8 = 0.18$ to 0.27); (2) deeper-living or outer shelf chaetognaths *Flaccisagitta hexaptera*, *Eukrohnia hamata*, *Pseudosagitta lyra*, *Mesosagitta decipiens*, and *Krohnitta subtilis* ($C_8 = 0.11$ to 0.30); and (3) the seasonal warm-water species *K. pacifica*, *Serratosagitta serratodentata*, *Ferosagitta hispida*, and *Sagitta tenuis* ($C_8 = 0.09$ to 0.26). *Sagitta helenae* and *Pterosagitta draco* shared positive associations with all three groups.

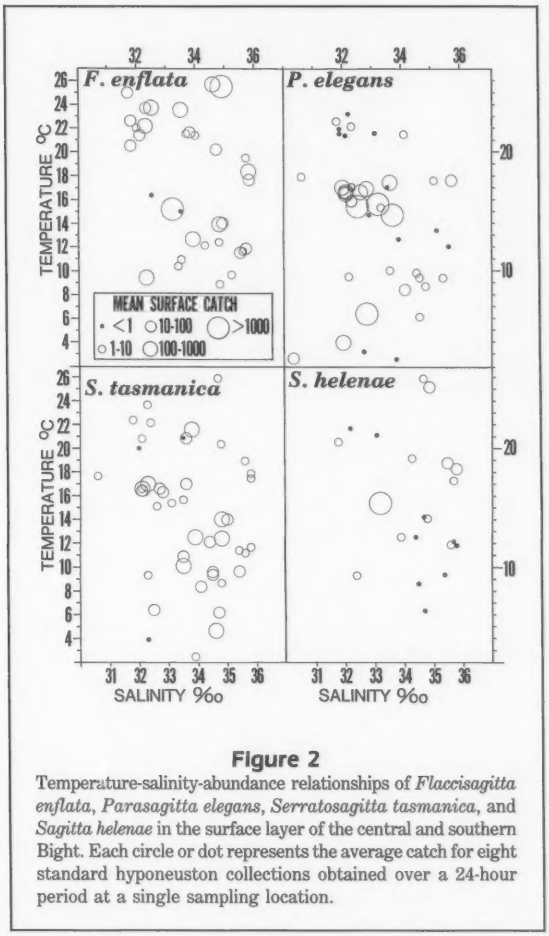


Figure 2

Temperature-salinity-abundance relationships of *Flaccisagitta enflata*, *Parasagitta elegans*, *Serratosagitta tasmanica*, and *Sagitta helenae* in the surface layer of the central and southern Bight. Each circle or dot represents the average catch for eight standard hyponeuston collections obtained over a 24-hour period at a single sampling location.

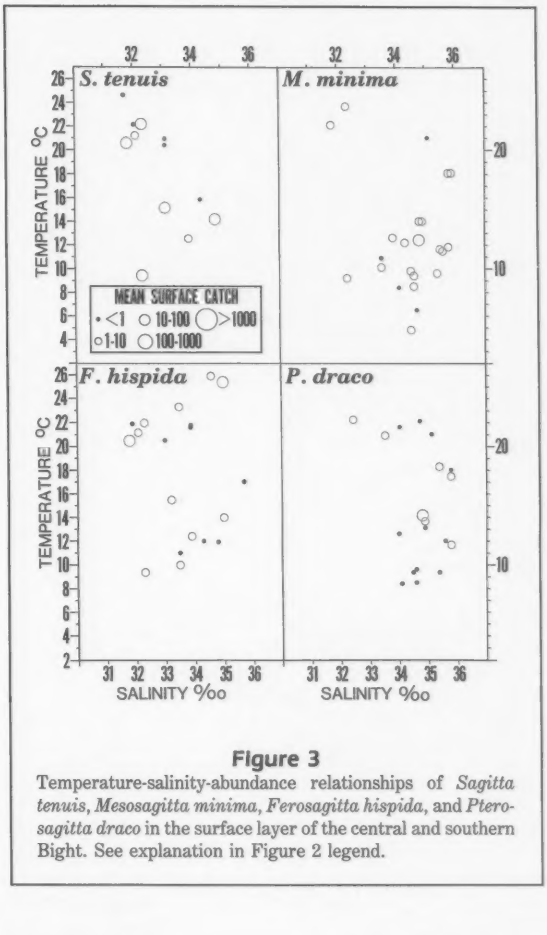


Figure 3

Temperature-salinity-abundance relationships of *Sagitta tenuis*, *Mesosagitta minima*, *Ferosagitta hispida*, and *Pterosagitta draco* in the surface layer of the central and southern Bight. See explanation in Figure 2 legend.

Diel distribution at the surface

Most of the chaetognaths commonly occurring in the surface layer reached peak densities near midnight (Table 6). *Flaccisagitta enflata*, *Krohnitta pacifica*, *Sagitta tenuis*, *Mesosagitta minima*, *Ferosagitta hispida*, and *Pterosagitta draco* all were caught in maximum numbers at that hour. Peak numbers of *Parasagitta elegans* and *Serratosagitta tasmanica* occurred somewhat earlier, but they were abundant throughout hours of darkness. There are also suggestions of dusk or dawn (or both) increases in abundance for *K. pacifica*, *F. hispida*, and *Serratosagitta serratodentata*.

Unlike any of the other chaetognaths, *Sagitta helenae* was decidedly more abundant at the surface in daylight hours, with 31.0 and 32.8% of total catches occurring around 1500 and 0900 hours, respectively.

Discussion

Eighteen species of chaetognaths are found in continental shelf waters of the Middle Atlantic Bight, including the 15 species on record after the 1960s plus the present records of three species previously known only from surface slope waters (Grice and Hart 1962). More recent studies of chaetognaths in this region have been restricted to estuaries (Grant 1977b, Sweatt 1980, Canino and Grant 1985) or to oceanic waters (Cheney 1985a, b). All of the western North Atlantic species labeled epipelagic or mesopelagic by Cheney (1985b) have been collected in shelf waters, so the present list appears reasonably complete. The composition of Middle Atlantic Bight chaetognath collections from hyponeuston and subsurface plankton tows was nearly identical. There were no frequent or abundant species unique to the hyponeuston, and all but the rarest species from subsurface shelf waters were taken at least occasionally from the surface layer. However,

Table 5

Number of occurrences (integers along the diagonal), coefficients of association (Hurlbert's C_s, right side of diagonal), and their statistical significance ($^{++}$ $P<0.01$ and $^{+}$ <0.05, respectively; blank = not significant, $P>0.05$, left side of diagonal) for chaetognaths collected during eight seasonal cruises in the Middle Atlantic Bight, 1975–77. Both subsurface and surface layer collections are included ($N = 716$); the three rarest species are excluded.

	pac	ser	his	ten	hel	dra	enf	min	tas	ele	ham	hex	lyr	dec	sub
Krohnitta pacifica	31	0.26	0.09	0	0.13	0.05	0.05	0	−0.09	−0.73	0	−1.00	0.04	0	0
Serratosagitta serratodentata	++	29	0.13	0	0.11	0.06	0.05	0.04	0.01	−0.19	0	0.04	0.05	0	0.05
Ferosagitta hispida	++	++	53	0.21	0	0.12	0.08	0.02	0.01	−0.64	−0.54	0.02	−1.00	0.02	0.03
Sagitta tenuis			++	46	0.09	0.07	0.08	−0.48	−0.18	−0.59	0	0	−1.00	0	0.02
Sagitta helenae	++	++		++	88	0.21	0.15	0.12	0.03	−0.40	0.06	−0.34	0.03	0.03	0.05
Pterosagitta draco		++	++		++	54	0.07	0.15	0.06	−0.22	0.13	0.09	0.05	0.08	0.09
Flaccisagitta enflata	++	++	++	++	++	++	322	0.22	0.18	−0.46	0.03	0.02	0.01	0.02	0.02
Mesosagitta minima		++		+	++	++	++	182	0.27	−0.15	0.08	0.08	0.05	0.03	0.04
Serratosagitta tasmanica		+			+	++	++	++	381	0.08	0.03	0.04	0.02	0.01	0.02
Parasagitta elegans	++		++	++	++		++	+	+	341	0.01	0	0	−0.27	0
Eukrohnia hamata					++	++	++	++	++		30	0.30	0.25	0.12	0.11
Flaccisagitta hexaptera						++		++	++		++	39	0.11	0.09	0.03
Pseudosagitta lyra		+				+	+	++	++		++	++	14	0.27	0.18
Mesosagitta decipiens						++	++	++	++		++	++	++	12	0.18
Krohnitta subtilis					++	++	++	++	++		++		++	++	15

Table 6

Diel distribution of the more common chaetognaths in hyponeuston collections. Data from 24-hour stations only, combined from eight seasonal cruises, 1975–1977.

	Hours (EST)								
	1200	1500	1800	2100	2400	0300	0600	0900	Total
	(% of total)								*N*
Flaccisagitta enflata	10.6	8.9	7.9	11.1	25.7	10.4	13.8	11.6	89,807
Parasagitta elegans	2.3	1.7	1.2	37.4	26.8	19.5	7.8	3.3	87,093
Serratosagitta tasmanica	1.3	1.3	6.7	30.3	27.9	23.5	6.2	2.8	16,283
Sagitta helenae	18.9	31.0	2.5	1.6	10.5	1.8	0.8	32.8	15,073
Krohnitta pacifica	3.5	10.3	11.8	2.5	34.0	1.9	23.0	13.1	2,573
Sagitta tenuis	0.5	0.9	10.3	13.7	45.2	18.2	7.9	3.3	2,283
Mesosagitta minima	0.9	1.4	2.4	8.9	60.4	13.6	7.5	4.9	1,383
Ferosagitta hispida	1.0	4.6	23.4	14.6	26.6	12.9	16.9	0	628
Serratosagitta serratodentata	0.2	2.9	28.2	8.3	0.7	3.4	56.2	0	411
Pterosagitta draco	0	0	1.7	11.9	32.2	27.1	26.3	0.8	118

there were apparent temperature-related differences in the percent frequency of chaetognath species in the two habitats. Cold-temperate species were less frequent at the surface than in the underlying water column, while warm-temperate or subtropical species were either equally frequent in the two habitats or more frequent in the hyponeuston.

The idea for T-S-P diagrams apparently originated with Pickford's (1946) study of the cephalopod *Vampyroteuthis*, and was first applied to chaetognaths by Bary (1959, 1963). T-S-P diagrams have since been used to relate abundance of chaetognaths to hydrography by numerous authors, including Sund (1961, 1964), Aurich (1971), Kotori (1976), Michel and Foyo (1976), O'Brien (1977), Nagasawa and Marumo (1982), and Andreu (1984). *Flaccisagitta enflata*, abundant in the Middle Atlantic Bight in warmer temperatures (averaging 18.6°C) and in various salinities (<32 to 36‰), occurred throughout the temperature and salinity ranges sampled by Nagasawa and Marumo (1982) and was apparently limited only by depth in the Caribbean (Michel and Foyo 1976). Sund (1961) also recorded *F. enflata* from 13–28°C and 32.6–35‰. T-S-P diagrams for *Parasagitta elegans* have been plotted by Bary (1963), who included the species in his "coastal (neritic) group," by O'Brien (1977) for populations to the west of Ireland, and by Kotori (1976) with ranges of temperature and salinity close to those in the present study. All agree in showing higher occurrence and abundance in colder water and an apparent tolerance for reduced salinity. Although the ranges of surface salinity in which Middle Atlantic Bight species were found were very similar, it is noteworthy that the five species with the lowest weighted means were the same five species recorded from within Chesapeake Bay (Grant 1977b) and in approximate inverse order of their estuarine abundance (*Sagitta tenuis*, $\bar{x}$ S = 32.6‰ and the most

abundant, to *Serratosagitta tasmanica*, $\bar{x}$ S = 33.7‰, the rarest in Chesapeake Bay). Aurich (1971) includes the only other known T-S-P diagram of *S. tasmanica*, used for a display of habitat differences with *S. serratodentata*. Michel and Foyo (1976) and Nagasawa and Marumo (1982) provided T-S-P diagrams for both *Mesosagitta minima* and *Pterosagitta draco*. Middle Atlantic Bight T-S-P diagrams agree with their depiction of greater abundance at higher salinities for these two species. Finally, Michel and Foyo's (1976) T-S-P diagram of *Ferosagitta hispida* shows a few occurrences at lower temperatures (13–17°C), but most at 27–28°C and in a broad range of salinities.

Association among the Middle Atlantic Bight species was generally positive, both in the multispecies case and between pairs of species. *Parasagitta elegans* provided an important and consistent exception, evidenced by its highly significant ($P<0.01$) negative associations with five warm-water species: *Krohnitta pacifica*, *Ferosagitta hispida*, *Sagitta tenuis*, *Flaccisagitta enflata*, and *Sagitta helenae*. Although both *P. elegans* and *S. tenuis* occur abundantly in coastal and estuarine waters in the Chesapeake region, they do so in opposite seasons, hence their negative association. The sole significant ($P<0.05$) positive association of *P. elegans* was with *Serratosagitta tasmanica*, and it appears to occupy a niche of low temperatures and salinities in this region, not unlike that of *Aidanosagitta crassa* in the East China Sea (Matsuzaki 1975). Highly significant positive associations were shared by (1) the endemic and abundant shelf species *Serratosagitta tasmanica*, *Mesosagitta minima*, and *Flaccisagitta enflata*, (2) the warm-water species *Krohnitta pacifica*, *Serratosagitta serratodentata*, *Ferosagitta hispida*, and *Sagitta tenuis*, and (3) the offshore, shelf-edge species *Flaccisagitta hexaptera*, *Eukrohnia hamata*, *Pseudosagitta lyra*, *Mesosagitta decipiens*, and *Krohnitta subtilis*. Three of the latter species comprised Matsuzaki's (1975) "Kuroshio water" species group.

Pearre (1973) determined that extensive diurnal migration takes place with *Parasagitta elegans*, perhaps related to feeding. Data in the present study on the diurnal distribution of the species in the hyponeuston also indicates a strong upward migration at night; numbers caught were about an order of magnitude higher at night than in daylight. Several other species showed similar sharp increases in abundance during darkness, including *Serratosagitta tasmanica*, *Krohnitta pacifica*, *Sagitta tenuis*, *Mesosagitta minima*, and *Pterosagitta draco*. Some were more abundant at dawn or dusk, or, in the case of *Flaccisagitta enflata* and *Sagitta helenae*, were present in considerable numbers in daylight. Among these species, Nagasawa and Marumo (1982) found evidence for diurnal migration in *F. enflata*, *P. draco*, and *K. subtilis*, none for *K. pacifica*, and mixed evidence for *M. minima* and *F. hexaptera*. However, in the present comparison of day and night hyponeuston collections, only a short migration would be required to populate and depopulate the surface layer diurnally. Such fine-scale diurnal movements likely do occur within the surface mixed layer, but are most difficult to measure.

Acknowledgments

Collections and identifications serving as the basis for this report were supported by the U.S. Dept. of the Interior, Bureau of Land Management Contracts No. 08550-CT-5-42 and AA550-CT6-62. Much appreciated were early and helpful reviews of this manuscript by Romuald N. Lipcius, Kenneth L. Webb, and Daniel W. Sved, and the suggestions by two anonymous reviewers for final alterations and adjustments.

Citations

Alvariño, A.
1963 Quetognatos epiplanctonocos del Mar de Cortes. Rev. Soc. Mex. Hist. Nat. 24:97–203 [in Spanish].

Andreu, P.
1984 *Sagitta decipiens* (Chaetognatha) en el Mediterraneo occidentale: Diagramas T-S plancton. Result. Exped. Cient. 12:23–30 [in Spanish, Engl. abstr.].

Aurich, H.J.
1971 Die Verbreitung der Chaetognathen im Gebiet des Nordatlantischen Strom-Systems. Ber. Dtsch. Wiss. Komm. Meeresforsch. 22:1–30 [in German, Engl. abstr.].

Bailey, N.T.J.
1981 Statistical methods in biology, 2d ed. John Wiley, NY, 216 p.

Bary, B. McK.
1959 Species of zooplankton as a means of identifying different surface waters and demonstrating their movements and mixing. Pac. Sci. 13:14–54.
1963 Temperature, salinity and plankton in the eastern North Atlantic and coastal waters of Britain, 1957. II. The relationships between species and water bodies. J. Fish. Res. Board Can. 20:1031–1066.

Bigelow, H.B., and M. Sears
1939 Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. Mem. Mus. Comp. Zool. Harv. Univ. 54:179–378.

Burrell, V.G. Jr., W.A. van Engel, and S.G. Hummel
1974 A new device for subsampling plankton samples. J. Cons. Perm. Int. Explor. Mer 35:364–367.

Canino, M.F., and G.C. Grant
1985 The feeding and diet of *Sagitta tenuis* (Chaetognatha) in the lower Chesapeake Bay. J. Plankton Res. 7:175–188.

Cheney, J.
1985a Spatial and temporal patterns of oceanic chaetognaths in the western North Atlantic — I. Hydrographic and seasonal abundance patterns. Deep-Sea Res. 32:1041–1059.
1985b Spatial and temporal patterns of oceanic chaetognaths in the western North Atlantic — II. Vertical distribution and migrations. Deep-Sea Res. 32:1061–1075.

Deevey, G.B.
1960 The zooplankton of the surface waters of the Delaware Bay region. Bull. Bingham Oceanogr. Collect. Yale Univ. 17:5–53.

Grant, G.C.
1963a Chaetognatha from inshore coastal waters off Delaware, and a northward extension of the known range of *Sagitta tenuis*. Chesapeake Sci. 4:36–42.
1963b Investigations of inner continental shelf waters off lower Chesapeake Bay. Part IV. Description of the Chaetognatha and a key to their identification. Chesapeake Sci. 4:107–119.
1967 The geographic distribution and taxonomic variation of *Sagitta serratodentata* Krohn 1853 and *Sagitta tasmanica* Thompson 1947 in the North Atlantic Ocean. Ph.D. diss., Univ. Rhode Island, Kingston, 116 p.
1977a Middle Atlantic Bight zooplankton: Seasonal bongo and neuston collections along a transect off southern New Jersey. Spec. Rep. ppl. Mar. Sci. Ocean Eng. (SRAMSOE) 173, Va. Inst. Mar. Sci., Gloucester Pt., 138 p.
1977b Seasonal distribution and abundance of the Chaetognatha in the lower Chesapeake Bay. Estuarine Coastal Mar. Sci. 5:809–824.
1979 Middle Atlantic Bight zooplankton: Second year results and a discussion of the two-year VIMS-BLM Survey. Spec. Rep. ppl. Mar. Sci. Ocean Eng. (SRAMSOE) 192, Va. Inst. Mar. Sci., Gloucester Pt., 236 p.
1988 Seasonal occurrence and dominance of *Centropages* congeners in the Middle Atlantic Bight, U.S.A. Hydrobiologia 167/168:227–237.

Grice, G.D., and A.D. Hart
1962 The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr. 32:287–309.

Hurlbert, S.H.
1969 A coefficient of interspecific association. Ecology 50: 1–9.

Kassatkina, A.P.
1971 New neritic species of chaetognaths from Possjet Bay in the Sea of Japan. Res. Mar. Fauna, Fauna and Flora of Possjet Bay, vol. 8, p. 265–294. Nauka Press, Leningrad [in Russian].

Kotori, M.
1976 The biology of Chaetognatha in the Bering Sea and the northern Pacific Ocean, with emphasis on *Sagitta elegans*. Mem. Fac. Fish., Hokkaido Univ. 23:95–183.

Ludwig, J.A., and J.F. Reynolds
1988 Statistical ecology. John Wiley, NY, 337 p.

Matsuzaki, M.
1975 On the distribution of chaetognaths in the East China Sea. The Oceanographical Mag. 26:57–62.

Michel, H.B., and M. Foyo
1976 Caribbean zooplankton. Part I. Siphonophora, Heteropoda, Copepoda, Euphausiacea, Chaetognatha and Salpidae. U.S. Dep. Navy, Office Naval Res., Wash., DC, 549 p.

Nagasawa, S., and R. Marumo
1982 Vertical distribution of epipelagic chaetognaths in Suruga Bay, Japan. Bull. Plankton Soc. Jpn. 29:9–23.

O'Brien, F.I.
1977 The relationship between temperature, salinity and Chaetognatha in the Galway Bay area of the west coast of Ireland. Proc. R. Ir. Acad. Sect. B Biol. Geol. Chem. Sci. 77:245–252.

Pearre, S.
1973 Vertical migration and feeding in *Sagitta elegans* Verrill. Ecology 54:300–314.

Pickford, G.E.
1946 *Vampyroteuthis infernalis* Chun. An archaic dibranchiate cephalopod. I. Natural history and distribution. Dana-Rep. Carlsburg Found. 26:197–210.

Pielou, E.C.
1977 Mathematical ecology. John Wiley, NY, 385 p.

Ratliff, R.D.
1982 A correction of Cole's C_7 and Hurlbert's C_8 coefficients of interspecific association. Ecology 63:1605–1606.

Schluter, D.
1984 A variance test for detecting species associations, with some example applications. Ecology 65:998–1005.

Sund, P.N.
1961 Some features of the autecology and distributions of Chaetognatha in the eastern tropical Pacific. Bull. Inter-Am. Trop. Tuna Comm. 5:305–340.
1964 The chaetognaths of the waters of the Peru region. Bull. Inter-Am. Trop. Tuna Comm. 9:113–216.

Sweatt, A.J.
1980 Chaetognaths in lower Narragansett Bay. Estuaries 3:106–110.

Tokioka, T.
1965 The taxonomical outline of Chaetognatha. Publ. Seto Mar. Biol. Lab. 12:335–357.

Zar, J.H.
1984 Biostatistical analysis, 2d ed. Prentice-Hall, Englewood Cliffs, NJ, 718 p.

Fishery-induced Changes in the Population Structure of Pink Shrimp *Pandalus jordani*

Robert W. Hannah
Stephen A. Jones

Oregon Department of Fish and Wildlife, Marine Region
Marine Science Drive, Bldg. 3, Newport, Oregon 97365

Abstract.—The trawl fishery for ocean pink shrimp (*Pandalus jordani* Rathbun) has increased dramatically since the early 1970s. Catch and effort statistics and catch sampling data from 1968-88 were analyzed to evaluate changes in the shrimp population structure. Carapace length at age one and two have increased significantly since 1978, concurrent with a reduction in fishery catch per unit effort, strongly indicating density-dependent growth. The seasonal pattern of growth provides further evidence for density-dependent growth. The number of age three shrimp in the catch has declined markedly since 1978, while age one shrimp have increased from 30.6% of the catch to 69.2%. The percentage of age one shrimp maturing as females has increased to 30-50% in some years, while the overall percentage of males shows no trend. The changes in growth, and age and sex composition of the catch are attributed in part to the impact of the trawl fishery, which is currently continuing to intensify. Density-dependent growth, and the ability to accelerate the sex change process make pink shrimp resistant to over-harvest. However, at some exploitation level the reduction of the age 1 spawning stock should begin to reduce subsequent recruitment. Recent strong year classes indicate that the fishery probably has not reached that level of exploitation.

Manuscript accepted 24 August 1990.
Fishery Bulletin, U.S. 89:41–51 (1991).

The Pacific trawl fishery for pink shrimp *Pandalus jordani* Rathbun has developed from a fishery with landings of around 220 mt in the early 1960s to a fishery regularly landing in excess of 18,000 mt. In six of the thirteen years since 1975, combined landings for the states of California, Washington, and Oregon have exceeded 24,000 mt. Pink shrimp range from San Diego, California to Unalaska, Alaska (Butler 1964); however, the majority of the catch is taken between Cape Mendocino, California and Destruction Island, Washington. The development of the fishery has been well summarized by Dahlstrom (1970), Fox (1972), Zirges and Robinson (1980), and others.

Saelens and Zirges (1985) described the 1984 fishery for pink shrimp and suggested that there was some evidence of changes in the shrimp population structure that were possibly the result of fishing. They noted improved growth and higher levels of age-1 shrimp in the catch, relative to earlier years. Fishing effort and shrimp catch have continued to increase since 1984. Given the continued development of this fishery, we felt that some fishery-induced changes in the population structure would be evident in a thorough review of the fishery sampling data. We examined 23 years of information from the pink shrimp fishery off the coasts of Oregon and northern California to search for the classic population responses to increased fishing. Specifically, we looked for persistent shifts in age and sex composition, changes in the age of female maturity, evidence of reduced stock biomass, and improved shrimp growth as a response to lower biomass. As a final step, we attempted to relate the observed changes to the development of the fishery and alternatively to environmental factors.

Methods

We examined monthly sample data from the landed catch of pink shrimp for the years 1966–88. The data is comprised of several samples from each statistical area (Fig. 1) and month of the fishing season. The season currently runs from April through October, but has been longer in the past. Individual samples for each area and month (area–month) were combined for analysis of age and sex composition. Sample summaries provide individual carapace lengths and average weight expressed as the number of whole shrimp per pound. Shrimp are classified as male, female, or transitional based upon close examination of the inner ramus of the first pleopod (Tegelberg and Smith 1957). Shrimp age is determined by modes in the combined length-frequency histogram (Zirges et al. 1981). Nadirs in the histograms define the range of carapace lengths corresponding to each age group, then ages are assigned to individual shrimp.

Zirges et al. (1982) concluded that pink shrimp from statistical areas

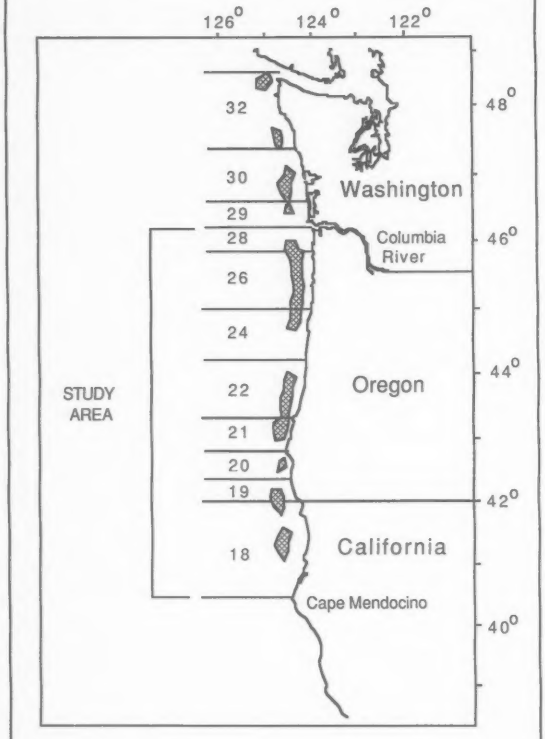


Figure 1
Location of commercial concentrations of pink shrimp *Pandalus jordani* along the U.S. Pacific coast (shaded areas) and statistical areas 18–32.

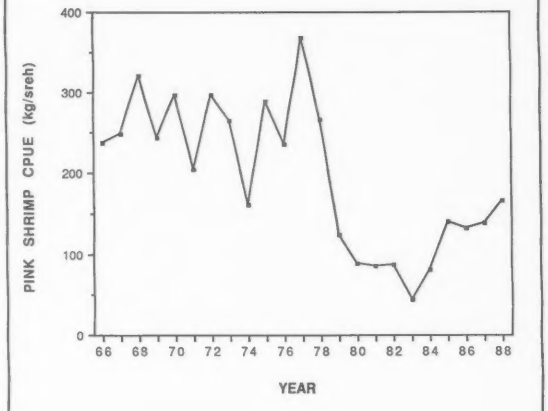


Figure 2
Catch-per-unit-effort (kg/single-rig equivalent hour) for the pink shrimp fishery in statistical areas 18–28 for the years 1966–88.

18–28 constituted a single stock, based upon an analysis of growth, maturation rates, and coastal oceanographic conditions. We used the same stock unit to allow us to draw upon the summarized sample data from Zirges et al. (1982) for the years 1966–81.

To evaluate the effect of shrimp density on growth, we compared shrimp carapace length at age for two time-periods representing different levels of population biomass. We use the term "density" in the sense of biomass per unit area rather than the number of individuals per unit area. We used catch-per-unit-effort (CPUE) as our index of shrimp density.

During the years 1975–78 major improvements in trawl design were implemented by the shrimp industry. Prior to 1976, the predominant shrimp net was a 57-foot (headrope) Gulf of Mexico style, Marinovitch trawl, with a 4-foot vertical opening (Zirges and Robinson 1980). During the years 1975–78 the majority of the fleet switched to locally produced 70–90 foot (headrope) box trawls. The new trawls have proven to be much more efficient for pink shrimp. Besides being generally bigger, they open to a height of 12–18 feet, improving fishing for pink shrimp, which come up off the bottom under reduced light conditions. Increased cloud cover and time of day were shown to bring concentrations of shrimp up off the bottom at least 8 feet (Beardsley 1973). The Oregon box trawls are also constructed differently from the Marinovitch trawls. They are much longer, employ a slower taper, and are hung with considerable "slack" webbing, all contributing to a much more efficient trawl for pink shrimp. The effort data series is not corrected for these gear improvements. Therefore, CPUE data understate the magnitude of biomass reduction since 1978 (Fig. 2). Accordingly, we tested growth for the two time-periods, 1966–78 and 1979–88. We considered these periods to be representative of the virgin stock biomass and the reduced biomass, respectively. We used F-tests to identify significant differences in length at age.

Four area–months were selected as indices for analysis of age-1 and -2 shrimp growth, based upon the completeness of the time-series data. For age-1 shrimp, the months of April–June were excluded because in some years age-1 shrimp are not fully recruited to the trawl gear in those months. For age-2 shrimp, the months of September and October were excluded because in recent years age-2 and older shrimp comprise a small percentage of late-season catches. Given these criteria, the index area–months selected for age-1 shrimp were

Area 22–August, Area 21–July, Area 26–August, and Area 19–August. The most complete time-series for age-2 shrimp were found to be Area 19–August, Area 22–April, Area 21–June, and Area 26–May. Age-2 length comparisons are not independent of the age-1 results. The age-2 analysis was employed to help rule out any apparent changes in growth of age-1 shrimp caused by changes in fishery or gear selectivity over time.

Table 1
Comparison of mean carapace length for age-1 and -2 pink shrimp for the years 1966–78 and 1979–88 (single classification ANOVA with unequal sample sizes).

Area–Month	Years	Mean carapace length (mm)	*N* (years)	*F* value	*P>F*
Age 1					
Area 22–August	1966–78	16.04	13	23.40	0.0001
	1979–88	17.32	7		
Area 21–July	1966–78	15.65	9	6.11	0.0251
	1979–88	16.44	9		
Area 26–August	1966–78	15.56	9	14.09	0.0021
	1979–88	16.67	7		
Area 19–August	1966–78	16.44	8	27.07	0.0002
	1979–88	17.79	7		
Age 2					
Area 19–August	1966–78	19.98	8	76.43	0.0001
	1979–88	21.84	7		
Area 22–April	1966–78	18.03	13	26.70	0.0001
	1979–88	19.59	9		
Area 21–June	1966–78	19.01	8	37.57	0.0001
	1979–88	20.60	9		
Area 26–May	1966–78	18.75	11	7.98	0.0112
	1979–88	19.69	9		

To further investigate factors influencing age-1 shrimp growth, we conducted some exploratory correlation analysis. Since the time-series for the most complete index areas still contained some missing samples, and since many of the environmental factors we wished to test are not area-specific, it was desirable to combine our four age-1 growth indices into one, more complete, time-series. Carapace length at age in pink shrimp exhibits a gradient effect increasing from north to south along the coast and also increasing through the season. To remove these effects and yet preserve the interannual variations in size, one of the four indices was chosen as a standard and the other three were adjusted by an additive factor equal to the difference between the mean of the chosen standard and that of the individual index area–month. Subsequently, the adjusted index area–months were averaged into one time-series. Area 22 was chosen as the standard, and the resultant time-series for age-1 was without gaps and most points were based on two or more adjusted means.

Linear regression was used to examine factors influencing variation in this age-1 shrimp growth index. The independent variables tested included sea surface temperature at Charleston, Oregon (Oreg. Dep. Fish. Wildl., unpubl. data) upwelling at 45°N, 125°W (Bakun 1973; NMFS Pacific Environ. Group, Monterey, CA, unpubl. data), inverse-barometer corrected sea level at Newport, Oregon, (Pittock et al. 1982; Pittock, unpubl. data), and catch per unit effort in the fishery as an index of shrimp density. Kruse (1981) found inverse barometer-corrected sea level at Newport and Neah Bay to be highly correlated with sea-bottom shelf temperatures near Newport. We tested each variable with no time lag (year t) and a 1-year time lag (t – 1) to match growth in an earlier life stage. Adjusted sea level at Newport was tested both with and without the 1983 data point, a year of abnormally high sea level caused by a strong El Niño event. Finally, we tested the average CPUE for the years t and t – 1 combined, to represent the average density encountered over the life of an age-1 shrimp. Second-order polynomial regression was also used to test each variable for a significantly curvilinear relationship with the age-1 growth index (Ricker 1975).

Correlation analysis with time-series data of short duration is often of limited value, but does help to generate initial hypotheses to be tested with the accumulation of future data (Ricker 1975). Short time-series often exhibit unidirectional time trends causing spurious correlations. For these reasons, we felt that correlation analysis would be a relatively poor tool for differentiating the relative importance of the various factors to shrimp growth, but would help to identify the factors which deserve future analysis. Consequently, correlation analysis was not pursued further in this study.

For analysis of trends in the sex composition data, we once again relied upon four index–area months with the most complete time-series. The four index–areas employed were Areas 19 and 28 in October and Areas 21 and 22 in September. Pink shrimp are protandrous hermaphrodites and mate primarily in September and October each year (Pacific Fisheries Management Council 1981). They usually mature first as males in the fall at about 1½ years of age, and after spawning

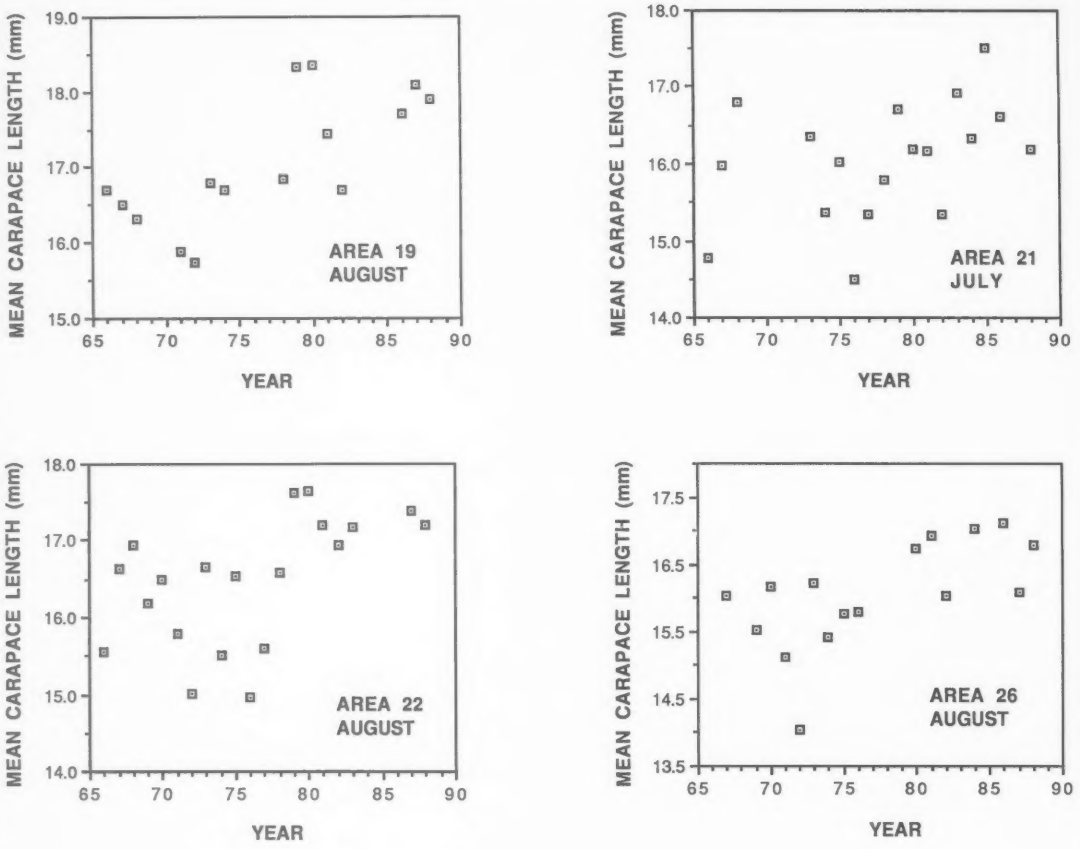


Figure 3
Mean carapace length of age-1 pink shrimp from 1966–88 for the selected index area–months.

go through a transitional phase, usually maturing as a female the following year at age 2½. Age-1 shrimp that mature directly into females, bypassing the male phase, are called primary females. We examined the data for trends in the percentage of primary females and the overall percentage of male shrimp.

Results

We found significantly improved growth of pink shrimp for the 1979–88 period as compared with the 1966–78 period. Mean carapace lengths for all four age-1 index area–months were significantly greater in 1979–88 (Table 1, Fig. 3) based on two-tailed F-tests. Mean carapace lengths were also greater for the four age-2 index area–months (Table 1, Fig. 4). Since age-2 shrimp are fully recruited to the trawl gear, this result rules out any apparent increase in mean length due to fishery or gear selectivity or accelerated sex change of age-1 shrimp. The time-series of catch per unit effort (Fig. 2) indicates that the population biomass has been reduced since 1978.

The increase in growth demonstrated for the 1979–88 catch years represents a substantial increase in average weight. Using the age-1 composite growth index, the mean carapace length of age-1 shrimp has increased from 16.1 to 17.4 mm. From the length-weight relationship developed by Zirges et al. (1982);

$$\ln W = -7.94746 + 3.2097 \ln L,$$

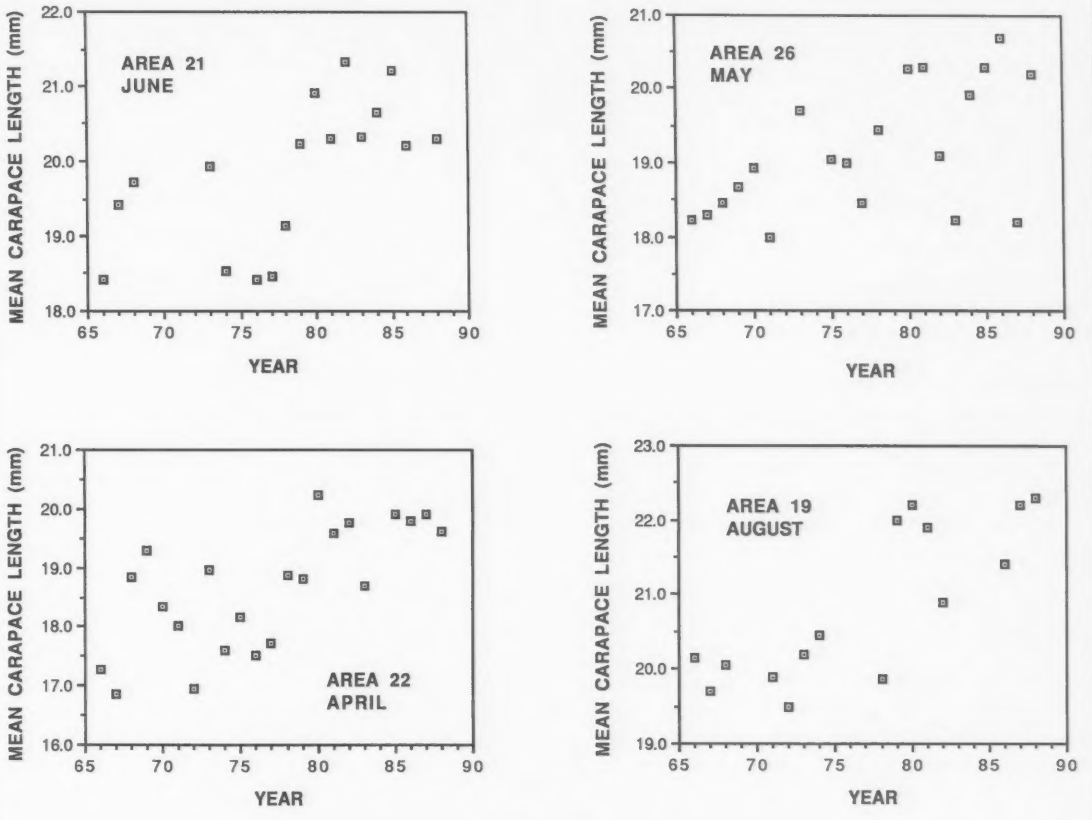


Figure 4
Mean carapace length of age-2 pink shrimp from 1966–88 for the four index area–months.

where W = Weight (g), and
L = Length (mm),

this represents a 28.4% increase in mean weight at age. This is an approximate figure scaled for Area 22 data; however, other areas yield similar results.

The exploratory correlation analysis (Table 2) shows that sea surface temperature at Charleston, Oregon, and sea level at Newport, Oregon (Fig. 5), are positively correlated with the age-1 growth index. However, CPUE (Fig. 6) is negatively correlated with the age-1 growth index suggesting density-dependent growth.

Adjusted sea level at Newport and sea surface temperature at Charleston displayed evidence of a curvilinear relationship, of decreasing slope, with the age-1 growth index. However, the regression coefficients of the second-order polynomial regressions were only significantly different from zero (t-test, $P>0.05$) for adjusted sea level in year t – 1. The curvature of this relationship is strongly influenced by a single outlier, the 1983 sea level, data point. With this point deleted, the coefficients of the polynomial regression are not significantly different from zero, while the adjusted r-squared value for the simple linear regression increases to 0.528 (Table 2). This suggests that bottom temperature is also influencing shrimp growth.

Graphs of mean length at age for areas 19, 21, 22 and 26 (Fig. 7) show that much of the difference in growth between the 1965–76 and 1977–86 broods is already apparent at age-13 months when the fishery first catches age-1 shrimp. This is not surprising, since density-dependent growth has been demonstrated more frequently for species during the immature phase, with density-dependent changes in fecundity more prevalent in the adult phase (Bailey and Almatar 1989). With the exception of area 19, the curves for the

1965–76 broods show some tendency for the rate of increase in length to slow in the fall, near the end of the fishing season, at ages 17–19 and 27–30 months. The curves for the 1977–86 broods differ somewhat in that this slowing of growth in the fall is less pronounced. These data suggest that density-dependent growth in pink shrimp may continue into the adult stage.

The impact that the trawl fishery has had upon the shrimp population is very evident from an examination of age composition of the catch (Fig. 8). In catch years 1966–78, age-3 shrimp comprised an average 20.4% of the catch by number, falling to an average 4.9% for the years 1979–88. Conversely, age-1 shrimp have risen from an average 30.6% in the early period to 69.2% of the catch in recent years. The increases in relative abundance of age-1 shrimp may be explained in part by the fact that they are recruited to the trawl gear earlier in the season due to increased size at age in recent years. The decline in absolute numbers of age-3 shrimp (Fig. 8) cannot be explained by changes in gear selection. The observed changes in age structure of the catch must be at least partly due to the impact of the trawl fishery.

The change in age composition of the catch is also reflected in the mean size of shrimp in the landed catch. The average number of shrimp per pound increased from 109.4 during the 1966–78 period to 118.9 for the 1979–88 period. The decline in numbers of older shrimp has been accompanied by an increase in the percentage of shrimp maturing directly into females at age-1 (Fig. 9). In recent years, levels of primary females as high as 30–50% are common. This effect has compensated for the higher cumulative harvest rates on age-2 and

Table 2

Results of exploratory regression analysis of potential factors influencing carapace length of age-1 pink shrimp. The dependent variable is an index of age-1 shrimp growth based upon mean carapace length from four selected statistical area–months.

Model	Independent variables*	Intercept	Coefficient	Adjusted r^2	P
1	U_t	—	—	—	NS
2	U_{t-1}	—	—	—	NS
3	SL_t	—	—	—	NS
4	SST_t	12.474	0.426	0.191	0.0307
5	SST_{t-1}	12.587	0.419	0.198	0.0323
6	SL_{t-1}	−20.096	0.125	0.348	0.0075
8	$CPUE_t$	17.709	−0.005	0.349	0.0018
7	$CPUE_{t-1}$	17.649	−0.005	0.287	0.006
9	Mean $CPUE_{t,t-1}$	17.877	−0.006	0.391	0.0009
10	SL_{t-1}**	−46.171	0.214	0.528	0.0009

*U = April–October upwelling from 45°N lat. 125°W long.
SL = Mean annual inverse-barometer corrected sea level at Newport, OR
SST = January–February mean sea surface temperature at Charleston, OR
CPUE = Catch-per-unit-effort for the pink shrimp fishery in statistical areas 18–28.
t = Calendar year of growth index.
**1983 sea level deleted.

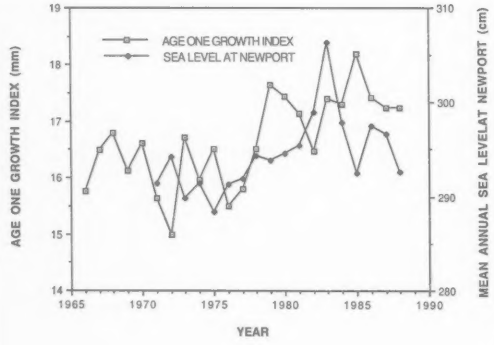


Figure 5

Age-1 growth index (mm) and mean inverse-barometer corrected sea level (cm) at Newport, Oregon for the years 1966–88 and 1971–88, respectively.

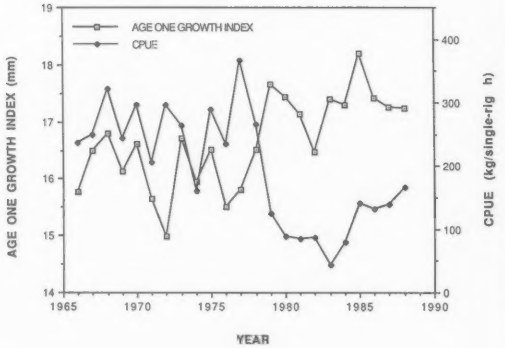


Figure 6

Age-1 growth index (mm) and pink shrimp catch-per-unit-effort (kg/single-rig equivalent hour) for 1966–88.

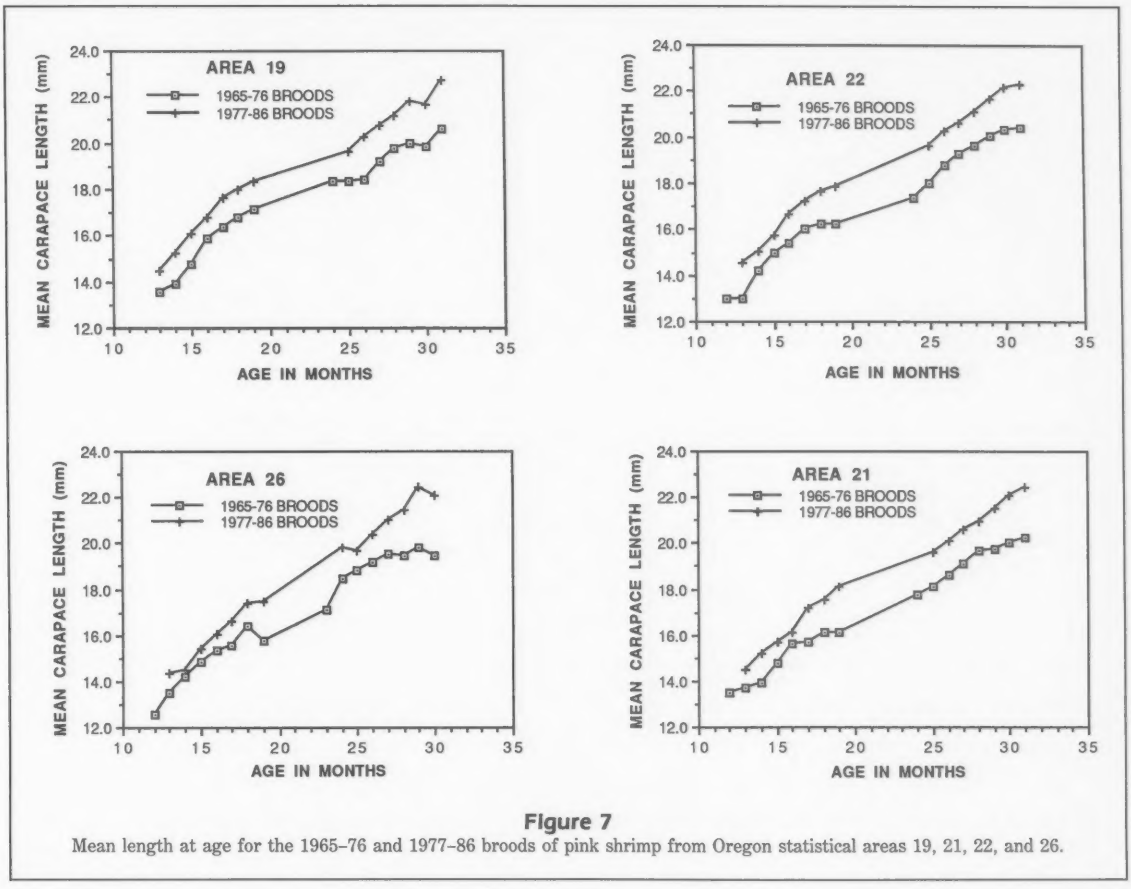


Figure 7
Mean length at age for the 1965–76 and 1977–86 broods of pink shrimp from Oregon statistical areas 19, 21, 22, and 26.

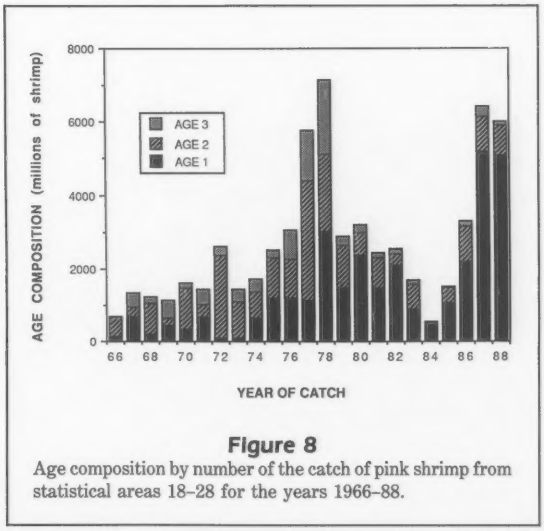


Figure 8
Age composition by number of the catch of pink shrimp from statistical areas 18–28 for the years 1966–88.

older shrimp, and a sexually balanced breeding population has been maintained (Fig. 10).

Discussion

Our analysis supports a conclusion that pink shrimp are exhibiting density-dependent growth. The transition to larger mean size at age between 1978 and 1979 coincides nearly exactly with the large drop in fishery CPUE, and the shift in age composition of the catch toward younger ages (Figs. 6, 8). This is probably due to the intensive development of the fishery during the mid 1970s (Fig. 11). The fishery continued to intensify after 1978, with subsequent effort levels falling to pre-1977 levels only in the years 1983–1985 (Fig. 12). The persistence of reduced CPUE and reduced mean age at capture are classic results of an intense size-selective harvest causing reduced levels of population biomass.

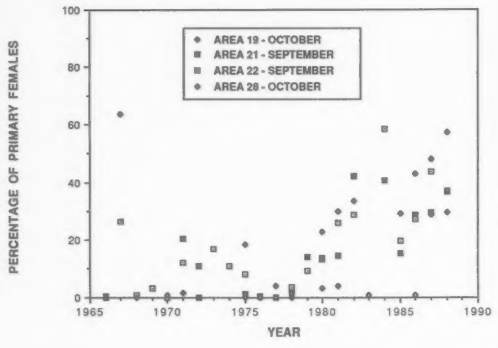


Figure 9
Percentage of age-1 pink shrimp maturing as females for four index area–months for the years 1966–88.

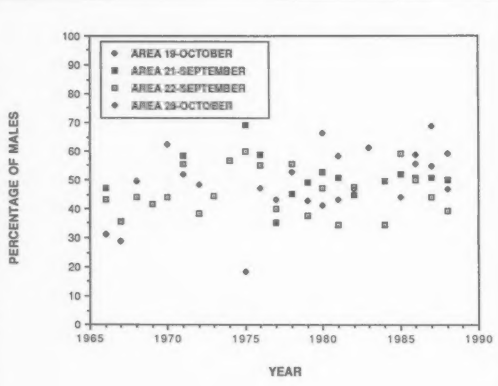


Figure 10
Percentage of male pink shrimp for four index area–months for the years 1966–88.

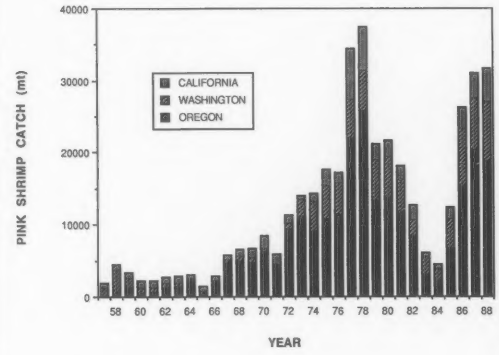


Figure 11
Combined landings of pink shrimp for the states of California, Oregon, and Washington for the years 1957–88.

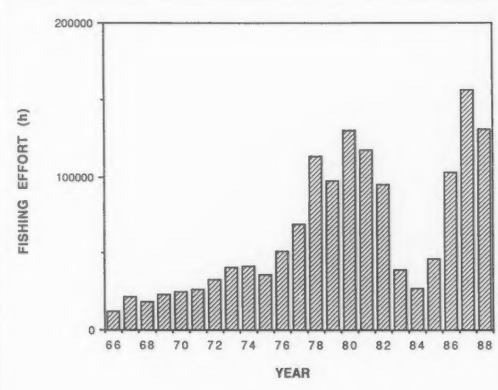


Figure 12
Fishing effort (single-rig equivalent hours) for pink shrimp in statistical areas 18–28 for the years 1966–88.

The pattern of growth in the index areas (Fig. 7) shows a slight tendency toward improved late-season growth in recent years, coincident with the season of minimum shrimp density on the grounds (Fig. 13). During the fall, age-0 shrimp begin to appear in the trawl catch in small numbers (Zirges et al. 1982). These data suggest that the improved growth occurring prior to age-13 months may be a result of decreased shrimp densities created by the trawl fishery.

The time-series of CPUE probably understates the true drop in shrimp biomass since 1978 due to the gear improvements mentioned previously. The difference in mean size at age demonstrated after 1979 may also be understated by the data shown in Figure 9. Prior to 1969 the minimum codend mesh allowed in the Oregon pink shrimp fishery was 38 mm (including one knot), while from 1969 onward codend mesh size has been unregulated (J.T. Golden, ODFW, Newport, 1981 draft). The lower curves in Figure 7, therefore, probably overestimate the mean size at age-1. Since 1979, with larger mean size, age-1 shrimp have been more completely sampled by the gear. D.R. Bernard (Oregon State Univ., Corvallis, 1983 draft) estimated that pink shrimp were fully recruited to the 38 mm mesh trawl

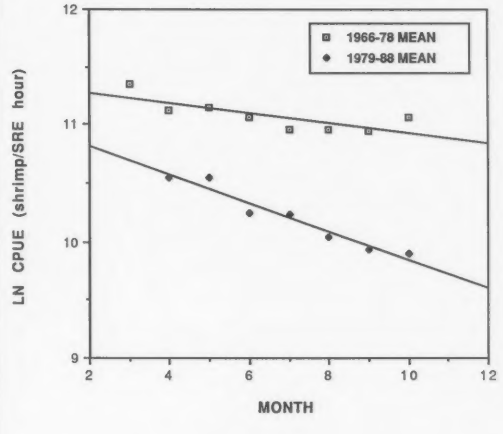


Figure 13
Log of mean catch-per-unit-effort (shrimp/single-rig equivalent hour) by month for 1966–78 and 1979–88.

at 16.6 mm carapace length. Since 1979, age-1 shrimp are fully recruited to a 38mm trawl in the later months of the season and to smaller gear even sooner. In earlier years, samples were biased toward only larger age-1 shrimp, and thus, by comparison, understate the increase in growth observed since 1979.

Our exploratory correlation analysis is inconclusive in differentiating between density-dependent and environmental factors as influences on shrimp growth. While the underlying relationship between the age-1 growth index and the environmental variables tested is most likely curvilinear (Ricker 1975), the relatively narrow range of environmental variability being tested in this case warranted the simple linear approximation. The combined age-1 growth index was closely correlated with our index of shrimp density, CPUE, despite the fact that CPUE is a relatively poor index of density. We showed CPUE to be negatively correlated with mean size at age over rather large changes in CPUE. Of course, smaller changes in CPUE, not associated with major changes in population density, should be positively correlated with growth, causing CPUE to be a poor index of shrimp density. We also found adjusted sea level at Newport, Oregon in year $t-1$ to be closely correlated with the age-1 growth index, indicating that warmer bottom temperatures may have caused improved shrimp growth after 1978. Rothlisberg (1975) showed shrimp growth to be positively correlated with temperature under laboratory conditions. It is possible that elevated sea levels improve growth over the normal range observed, but at extreme levels such as occurred in 1983, the virtual complete shutdown of coastal upwelling has the reverse effect (Pearcy et al. 1985, Miller et al. 1985).

The hypothesis that sea surface or bottom temperatures (as inferred from sea level data) are controlling shrimp growth will most likely be tested over the next decade or two. In time, the relatively warm ocean conditions experienced off the Oregon coast since 1978 will probably be replaced by a colder, upwelling-dominated regime, similar to the early 1970s. The mean increase in length we have measured is equivalent to a 28% increase in average weight at age. If sea-bottom temperatures are controlling growth and return to lower levels, the drop in fishery yield will be profound. Conversely, it is unlikely that the shrimp fishery will be substantially reduced, allowing standing stocks of shrimp to rebuild to near virgin levels of the early 1970s. Thus, as we see the subsequent trend in mean carapace length at age of pink shrimp, our hypothesis of density-dependent growth will be tested further.

Charnov et al. (1981) showed that reductions in the population of age-2 and older shrimp (predominantly female) should result in increases in primary females. If Charnov is correct, the trawl fishery, through selective removal of older shrimp, should be causing this effect in the population. The result of accelerated sex change should be higher levels of primary females and a roughly stable sex ratio. Jensen (1965) and Charnov (1980) noted increased levels of young females in *Pandalus borealis* populations after intensive fishery development.

We question what these changes in population structure imply for the future productivity of the pink shrimp resource. The evidence for density-dependent growth argues for a harvest-resistant shrimp stock. Our data also support the hypothesis of Charnov et al. (1978) that the population age structure determines the age of sex change in shrimp. As a consequence of intensive harvest, the age structure has shifted toward younger shrimp. The percentage of primary females has increased, however, resulting in the maintenance of a sexually balanced breeding population. The capacity to accelerate sex change in pink shrimp also increases the stock's ability to withstand harvest pressure, by decreasing the potential for declines in larval production.

Both catch and effort levels in the pink shrimp fishery are continuing to increase. The preliminary total catch for the states of California, Oregon, and Washington is nearly 36,000 mt in 1989. The large harvests in 1987–89 (Fig. 11) appear to be the result of a combination of factors. Improved CPUE in 1987 and 1988 (Fig. 2; 1989 data unavailable) indicate some strong year classes of shrimp moving through the fishery. The total harvest levels of age-1 shrimp in these years is

unprecedented in the history of the fishery. The increased size of age-1 shrimp since 1979 has made them more vulnerable to the gear and should have increased the harvest rate on age-1 shrimp relative to 1966–78. Fishing effort in the study area in 1987 and 1988 reached the two highest totals ever recorded, with 1989 likely to be as high or higher. The only other year in which effort approached levels of 1987–88 was in 1980 (Fig. 12). Postulating some improvement in vessel and gear efficiency in the years since 1980, the strong landings of 1987–89 must have been partly a result of record levels of effective fishing effort. In combination, the strong landings, high effort, and dominance of age 1 shrimp in the catch for 1987 and 1988 argue strongly for increased exploitation rates in those years. The large landings in 1989 are probably caused by the same factors.

This raises the question of what impact the increasing harvest of age-1 shrimp may have on the spawning population and subsequent recruitments. A spawner-recruit relationship has not been demonstrated for pink shrimp (Gotshall 1972). However, the Pacific Fishery Management Council (1981) identified some potential indicators of over-harvest of shrimp stocks. These included increases in the percentage of age-1 shrimp in the catch and in the percentage of primary females. In the past, reductions in age-2 and older shrimp were balanced by accelerated sex change in age-1 shrimp, and possibly by increased fecundity at age due to density-dependent growth. Levels of primary females have reached nearly 50% in some years. In such years, pink shrimp are virtually a single-age spawning stock. At some level of exploitation, accelerated sex change and density-dependent growth will not prevent declines in larval release and subsequent recruitment. The strong year-classes passing through the fishery since 1986 indicate that we've probably not reached that level of exploitation as yet.

Acknowledgments

This project was financed in part with Federal Interjurisdictional Fisheries Act funds through the U.S. National Marine Fisheries Service. Numerous individuals provided assistance in the completion of this project. P. Collier of the California Department of Fish and Game and M. Gross of the Washington Department of Fisheries provided unpublished data used in our analysis. J. Robinson, J. Golden, R. Starr, and M. Saelens provided historical background information on the shrimp fishery. The draft manuscript was reviewed by R. Starr and also by D. Hankin of Humboldt State University. Assistance on statistical questions was provided by P. Lawson.

Citations

Bakun A.
1973 Coast upwelling indices, west coast of North America 1946–71. NOAA Tech. Rep. NMFS SSRF-671, 103 p.

Beardsley A.
1973 Design and evaluation of a sampler for measuring the near-bottom vertical distribution of pink shrimp (*Pandalus jordani*). Fish. Bull., U.S. 71:243–253.

Bailey, R.S., and S.M. Almatar
1989 Variation in the fecundity and egg weight of herring (*Clupea harengus* L.). Part II. Implications for hypotheses on the stability of marine fish populations. J. Cons. Cons. Int. Explor. Mer 45:125–130.

Butler, T.H.
1964 Growth, reproduction, and distribution of pandalid shrimps in British Columbia. J. Fish. Res. Board Can. 21: 1403–1452.

Charnov, E.L.
1981 Sex reversal in *Pandalus borealis*: Effect of a shrimp fishery? Mar. Biol. Lett. 2 (1981):53–57.

Charnov, E.L., D.W. Gotshall, and J.G. Robinson
1978 Sex ratio: Adaptive response to population fluctuations in pandalid shrimp. Science (Wash. DC) 200:204–206.

Dahlstrom, W.A.
1970 Synopsis of biological data on the ocean shrimp *Pandalus jordani*, Rathbun, 1902. FAO Fish. Rep. 57(4):1377–1416.

Fox, W.W.
1972 Dynamics of exploited pandalid shrimps and an evaluation of management models. Ph.D. diss., Univ. Wash., Seattle, 148 p.

Gotshall, D.W.
1972 Population size, mortality rates, and growth rates of northern California ocean shrimp *Pandalus jordani*, 1965 through 1968. Calif. Dep. Fish Game, Fish Bull. 155:1–47.

Jensen, A.J.
1965 *Pandalus borealis* in the Skagerak (length, growth and changes in the stock and fishery yield). Rapp. P.-V. Reun. Cons. Int. Explor. Mer 156:109–111.

Kruse, G.H.
1981 Relationship between shelf temperatures, coastal sea level, the coastal upwelling index, and English sole (*Parophrys vetulus*) spawning activity off Oregon. M.S. thesis, Oregon State Univ., Corvallis, 68 p.

Miller, C.B., H.P. Batchelder, R.D. Brodeur, and W.G. Pearcy
1985 Responses of the zooplankton and ichthyoplankton off Oregon to the El Niño event of 1983. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño north: Niño effects in the eastern subarctic Pacific ocean, p. 184–187. Wash. Sea Grant Prog., Univ. Wash., Seattle.

Pacific Fishery Management Council
1981 Discussion draft fishery management plan for the pink shrimp fishery off Washington, Oregon, and California. Pac. Fish. Manage. Counc., Portland, 169 p.

Pearcy, W.G., J. Fisher, R. Brodeur, and S. Johnson
1985 Effects of the 1983 El Niño on coastal nekton off Oregon and Washington. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño north: Niño effects in the eastern subarctic Pacific ocean, p. 188–204. Wash. Sea Grant Prog., Univ. Wash., Seattle.

Pittock, H.L., W.E. Gilbert, A. Hyer, and R.L. Smith
1982 Observations of sea level, wind, and atmospheric pressure at Newport, Oregon, 1967–1980. Natl. Sci. Found. Data Rep. 98 Ref. 82-12, Oreg. State Univ., Corvallis, 158 p.

Ricker, W.E.
1975 Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191, 322 p.
Rothlisberg, P.C.
1975 Larval ecology of *Pandalus jordani* Rathbun. Ph.D. diss., Oreg. State Univ., Corvallis, 117 p.
Saelens, M.R., and M.H. Zirges
1985 The 1984 Oregon shrimp fishery. Inf. Rep. 85-6, Oregon Dep. Fish Wildl., Newport, 29 p.
Tegelberg, H.C., and J.M. Smith
1957 Observations on the distribution and biology of the pink shrimp (*Pandalus jordani*) off the Washington coast. Wash. Dep. Fish. Res. Pap. 2(1):25–34.
Zirges, M.H., and J.G. Robinson
1980 The Oregon pink shrimp fishery, management history and research activities. Inf. Rep. Ser. Fish. 80-1, Oregon Dep. Fish Wildl., Newport, 15 p.
Zirges, M.H., M.R. Saelens, and J.E. McCrae
1981 Length-frequency, size, sex, and age composition data by month and area for pink shrimp landed in Oregon 1966 to 1980. Inf. Rep. Ser. Fish 81-2, Oregon Dep. Fish Wildl., Newport, 348 p.
1982 Total catch and effort tables, and summary biological statistics for pink shrimp caught in Oregon statistical areas 18–28 by month and area 1966–1981; catch numbers expanded by age and sex, effort in hours by vessel type. Inf. Rep. Ser. Fish. 82-4, Oregon Dep. Fish Wildl., Newport, 145 p.

Between-Reader Bias and Variability in the Age-Determination Process

Daniel K. Kimura
Julaine J. Lyons

Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, Seattle, Washington 98115-0070

Abstract.– At the Alaska Fisheries Science Center, one in five age readings produced for routine stock assessments are re-aged independently by a second age-reader. The Center now has a large database of repeated age readings that covers a variety of groundfish species and years. The purpose of this paper is to point out the problems and utility of interpreting such a database. The main problem of interpretation is fundamental, and relates to the fact that the true age of a fish is seldom known. Nevertheless, from a pragmatic point of view, these data can still provide useful insights into the age-determination process. Data from six marine fish species are used to show the overall levels of between-reader bias, agreement, and variability that have occurred on production age readings. Other uses for these data include objectively ranking the relative difficulty in ageing different species, maintaining quality control, examining between-reader differences in ageing criteria, and evaluating the possible importance of between-reader bias and variability in later analysis and modeling applications. Assuming reader bias is negligible, modeling results presented here indicate that estimated percentage agreements are consistent with the hypothesis that age determinations are normally distributed with a constant coefficient of variation over relatively wide age ranges. This result supports use of the coefficient of variation for measuring variability in age precision studies.

Manuscript accepted 6 August 1990.
Fishery Bulletin, U.S. 89:53–60 (1991).

In this paper we evaluate a unique database developed for all marine fish species being routinely aged at the Alaska Fisheries Science Center. Here, large subsamples (one in five age readings produced for routine stock assessments) have been re-aged independently by a second experienced age-reader, mainly for the purpose of maintaining quality control. However, it became apparent that this database could be used to provide additional insights into the age-determination process.

Most everyone familiar with the ageing of fish knows this process is fraught with difficulties. At the very least, there must be random variability about some true age. Most likely there is also bias in the ageing methodology at some ages, as well as between-reader differences. Because reader bias is probably affected by the individual reader, the true age of the fish being aged, and perhaps even individual fish, the analysis of repeated age readings made by different readers does not easily fall under the purview of classical statistical theory.

The types of analysis that can be performed on age-determination data are dependent on the kind of data collected and the assumptions the data analyst is willing to make. For example, if replicated readings are made by each reader, it is possible to perform a variance components analysis, assuming that reader effects are random and unbiased (Kimura et al. 1979). Comparative calibration is the area of statistical analysis that compares different methods of measurement (e.g., different readers) where all methods of measurement are assumed to contain error, and perhaps bias (Theobald and Mallinson 1978). Recently Kimura (unpubl.) examined the limits of possible inference for the functional comparative calibration model.

In the analyses presented here we examine between-reader bias and variability based on subsamples aged independently by two age-readers. For these types of data, we define between-reader bias as the average difference $(\bar{a}_1 - \bar{a}_2)$ in ages assigned by these readers when ageing the same specimens of the same nominal age. Thus between-reader bias presumably arises from the two readers using different ageing criteria. If the average difference between age-readers is negligible at some nominal age, then between-reader bias at that age is defined to be negligible, regardless of what the unknown absolute bias of the readers might be.

Estimates of between-reader ageing variability from these types of data can be computed by averaging the sample variances calculated from the two age readings ($df = 1$) from each age structure over some nominal age. These sample variances (between-reader variances) probably overestimate measurement error, because they include a component of variability that might be thought of as between-reader bias.

Age determination is a statistical process that has a characteristic level of variability. This variability is species-dependent, and provides a basis for comparing the ageing of different

species. For example, a species that can be aged with a larger percentage agreement (percentage of specimens aged the same on two occasions by the same or different reader), or smaller coefficient of variation, provides a statistical confirmation of the statement that species "x" is easier to age than species "y."

Between-reader bias provides a measure of the adequacy of criteria for distinguishing ages in a particular species of some nominal age. Presumably, if there is no between-reader bias, ageing criteria are being applied similarly by both readers, and the data only contain random measurement error. If between-reader bias and measurement error are independent, at this point between-reader variance would also be minimized. Significant between-reader bias may indicate a lack of resolving power in the criteria, insufficient training, or even peculiarities in the structures being aged. Between-reader variance is generally an indicator of overall "ageability," but is not as effective as between-reader bias measurements for pointing out between-reader differences in criteria.

Species often have a characteristic age above which between-reader biases become larger. This age may be interpreted as a line distinguishing which ages are more reliable. For age-readers themselves, between-reader bias is usually of more interest than variability. This is because while measurement error is inherent in the age-determination process, between-reader bias can be controlled to a greater extent.

In age-determination studies the term "precision" is used to describe "agreement," or variability between readings of the same specimen by the same or different age-reader. The term "accuracy" is reserved to describe a comparison of ages generated by readers with the "true" age for specimens of known age.

By emphasizing the importance of between-reader bias and variability, we do not mean to denigrate the obvious importance accuracy and age validation play in the age-determination process (Beamish and McFarlane 1983, 1987). Validation (the comparison of ages determined by counting rings on hard parts with known ages) can be carried out in a variety of ways, all of which are difficult. These include combining an external tag with an oxytetracycline (OTC) injection that labels calcium rings with a mark visible under ultraviolet light, following unusually strong year-classes through time, ageing young fish of known ages, and, most recently, measuring the activity of naturally occurring radioisotopes. Scientists at the Pacific Biological Station (Beamish et al. 1983, Cass and Beamish 1983, Leaman and Nagtegaal 1987, McFarlane and Beamish 1987) have made wide use of the OTC mark. And, recently, two studies appear to have succeeded in validating longevity in rockfish using radioisotopes (Bennett et al. 1982, Campana et al. 1990). Typically, validation can be carried out on only a very few fish. Often, doubts remain concerning criteria for certain age groups, or structures that look different. Nevertheless, the validation process is a critical one, and age-readers must constantly strive to improve the accuracy of their age determinations.

Because we seldom knew the true age of a fish, absolute bias and total mean-square error in the ageing process were not known. Therefore, our discussions here will be limited to between-reader bias and variability. These quantities are defined by the between-reader bias and coefficient-of-variation formulas described in the following section.

Materials and methods

The Ageing Unit at the Alaska Fisheries Science Center has the broad responsibility of ageing commercially important fish species and fish stocks in U.S. waters from California to the eastern Bering Sea. Historically, data have been accumulated from three principal sources: scientific surveys using various fishing gear, and foreign and domestic vessels fishing in U.S. waters. The present data consist of ages read from the otoliths (ear bones) of various groundfish species collected using assorted gear.

Since 1981, the preferred method of reading ages from these structures has been to either break or saw the otolith cross-wise, burn the exposed surface, and read the cross-section under a microscope (Chilton and Beamish 1982). Only young or unusually clear specimens of select species can be read from the intact surface.

In 1983 a quality-control program was initiated wherein 20% of all routine age readings would be independently re-aged by an age-reader (i.e., the tester) particularly experienced in a species. Statistics were calculated on these reader/tester data (one reading per otolith from each age-reader) in the following manner:

1 mean ($\bar{x}$) = (tester + reader)/2.
2 standard deviation (SD) = $\sqrt{[(\text{tester} - \bar{x})^2 + (\text{reader} - \bar{x})^2]}$
3 nominal age (age): $\bar{x}$ (rounded), or tester age
4 n (count): sample size (number of specimens aged)
5 percentage agreement: (n agree/n) × 100
6 coefficient of variation (CV) = (SD/$\bar{x}$) × 100
7 between-reader bias: reader age − tester age
8 percentage bias: [(reader age − tester age)/$\bar{x}$] × 100

Elements 5–8 were averaged over the "n" specimens of the same nominal age, and over all ages (weighted by n) for overall statistics.

Table 1
Statistics comparing reader/tester data for Pacific whiting in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
2	258	100.0	0.0	0.00	0.0
3	58	50.0	15.1	−0.14	−5.3
4	8	62.5	7.6	−0.38	−10.7
5	13	92.3	3.6	0.23	5.1
6	651	95.5	0.6	−0.00	−0.2
7	118	20.3	9.9	0.23	3.4
8	66	37.9	11.9	−0.23	−2.9
9	153	77.8	2.4	−0.02	−0.2
10	28	10.7	12.1	0.25	2.4
11	23	26.1	12.0	0.00	−0.2
12	13	0.0	12.0	−0.92	−7.9
13	29	75.9	1.4	0.03	0.3
14	11	0.0	6.1	0.45	3.3
15	4	25.0	13.1	0.25	1.5
16	2	100.0	0.0	0.00	0.0
Average		78.6	3.2		

Table 2
Statistics comparing reader/tester data for yellowfin sole in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
3	1	100.0	0.0	0.00	0.0
4	4	50.0	10.1	0.50	14.3
5	11	45.5	9.7	0.64	13.7
6	15	86.7	1.7	0.13	2.4
7	64	79.7	2.2	0.14	2.2
8	32	68.8	2.9	0.06	0.8
9	23	78.3	1.8	−0.13	−1.5
10	39	66.7	2.7	0.21	2.1
11	19	57.9	3.2	−0.16	−1.5
12	32	62.5	3.0	0.25	2.1
13	19	52.6	3.3	−0.05	−0.4
14	14	42.9	6.9	0.79	5.7
15	22	68.2	2.2	0.45	3.1
16	26	34.6	3.6	0.04	0.2
17	12	25.0	5.3	0.08	0.5
18	16	43.8	3.0	0.38	2.2
19	12	58.3	1.9	0.33	1.8
20	5	0.0	7.1	0.00	0.0
23	3	0.0	5.1	−1.00	−4.3
25	1	0.0	2.9	1.00	4.1
26	1	0.0	2.8	1.00	3.9
Average		60.9	3.2		

When the main purpose of an analysis is to compare criteria of the age readers, the nominal age for classification should be the tester age. When the overall characteristics of ageing a species is of interest, perhaps $\bar{x}$ is the better nominal age. The estimated statistics by age look different depending on which nominal age is being used. For example, if $\bar{x}$ is used, the percentage agreement for younger ages will appear larger.

Both the average percent error (Beamish and Fournier 1981) and the coefficient of variation have been proposed as an "age independent" method of estimating precision for age-determination studies. Assuming normality, Chang (1982) favored the coefficient of variation on the basis of efficiency, and we favor the coefficient of variation on the basis of common usage. Under differing distributional assumptions, the average percent error may actually be superior.

If age determinations are independently and normally distributed about some true age, then the percentage agreement at each age can be predicted from the area under the normal curve. Suppose the age of an "a"-year-old fish can be determined with a certain coefficient of variation. The difference between two independent age determinations (b and c, say), would be distributed as

$$z = b - c \sim N[0, 2CV^2a^2].$$

The predicted percentage agreement (ppa) at age "a" is then

$$ppa = [\Phi(z_2) - \Phi(z_1)] \times 100,$$

where Φ = the cumulative distribution function of the unit normal distribution,
$z_1 = -0.5/[(1.4142)(CV)(a)]$ and,
$z_2 = +0.5/[(1.4142)(CV)(a)]$.

Results and discussion

The above statistics were calculated for several species sampled in 1986 and subsequently aged (Tables 1–6). These are overall statistics calculated using data from all readers and testers, and therefore represent group rather than individual performance. A summary of percentage agreements and coefficients of variation averaged over all ages is given below:

Species	Percentage agreement	CV
Pacific whiting *Merluccius productus*	78.6	0.032
yellowfin sole *Limanda aspera*	60.9	0.032
Pacific ocean perch *Sebastes alutus*	40.8	0.049
walleye pollock *Theragra chalcogramma*	63.8	0.050
Atka mackerel *Pleurogrammus monopterygius*	66.8	0.068
sablefish *Anoplopoma fimbria*	43.7	0.129

Table 3

Statistics comparing reader/tester data for Pacific ocean perch in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias	Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
2	1	100.0	0.0	0.00	0.0	34	2	0.0	12.7	1.00	3.0
3	7	71.4	8.1	0.29	11.4	36	1	0.0	3.9	−2.00	−5.6
4	1	0.0	20.2	1.00	28.6	37	2	0.0	1.9	1.00	2.7
5	34	73.5	4.2	−0.03	−0.7	38	3	66.7	0.6	0.33	0.9
6	29	51.7	6.2	−0.28	−5.0	39	5	0.0	8.0	0.80	2.0
7	9	33.3	10.7	−0.78	−11.7	40	2	0.0	2.7	−1.50	−3.8
8	62	71.0	2.9	0.02	0.2	41	8	12.5	2.2	−0.50	−1.2
9	42	45.2	4.7	0.05	0.5	42	6	50.0	1.7	0.00	0.0
10	41	36.6	5.8	0.20	2.1	43	4	25.0	3.7	0.75	1.7
11	12	25.0	7.7	0.33	3.1	44	1	0.0	4.9	3.00	6.9
12	21	38.1	5.2	0.19	1.6	45	3	66.7	1.0	0.67	1.5
13	6	16.7	7.3	−0.67	−5.2	46	3	0.0	2.1	−0.67	−1.4
14	8	0.0	6.5	−1.00	−7.3	47	1	0.0	3.0	2.00	4.3
15	9	33.3	5.3	0.44	3.0	48	1	100.0	0.0	0.00	0.0
16	14	21.4	4.8	0.50	3.2	49	1	0.0	1.5	1.00	2.1
17	5	20.0	5.0	0.40	2.4	50	2	0.0	1.4	0.00	0.0
18	7	14.3	6.8	0.00	−0.0	52	5	0.0	7.4	4.20	8.1
19	8	37.5	7.0	1.13	5.9	54	2	0.0	2.6	−1.00	−1.9
20	7	28.6	4.6	−0.71	−3.7	55	2	50.0	3.2	−2.50	−4.6
21	1	0.0	10.3	3.00	14.6	56	1	0.0	3.8	3.00	5.4
22	1	100.0	0.0	0.00	0.0	57	2	0.0	7.4	−6.00	−10.5
23	2	0.0	6.1	0.00	0.0	59	3	0.0	6.0	−3.00	−5.1
24	2	50.0	1.5	−0.50	−2.1	60	1	0.0	2.4	−2.00	−3.3
25	4	25.0	4.3	−1.50	−6.1	61	5	0.0	2.8	−1.60	−2.6
26	2	0.0	2.8	0.00	0.0	65	2	50.0	1.6	−1.50	−2.3
27	3	33.3	3.6	1.33	5.0	66	1	0.0	1.1	−1.00	−1.5
28	2	100.0	0.0	0.00	0.0	68	1	0.0	3.1	3.00	4.4
29	2	0.0	17.1	3.00	10.3	72	1	0.0	1.0	1.00	1.4
30	1	0.0	4.7	2.00	6.7	73	1	0.0	8.8	9.00	12.4
31	2	0.0	4.6	0.00	0.0	75	1	100.0	0.0	0.00	0.0
32	2	0.0	4.4	0.00	0.0	78	1	0.0	3.6	−4.00	−5.1
33	1	100.0	0.0	0.00	0.0	Average		40.8	4.9		

Table 4

Statistics comparing reader/tester data for pollock in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
1	18	100.0	0.0	0.00	0.0
2	64	93.8	2.9	0.03	2.1
3	132	92.4	2.1	0.00	0.0
4	159	74.8	5.3	0.04	1.0
5	136	66.2	5.6	0.07	1.5
6	119	64.7	5.2	0.06	1.1
7	113	49.6	6.5	−0.19	−2.7
8	181	56.9	4.7	−0.19	−2.5
9	85	21.2	7.1	0.11	1.2
10	26	15.4	10.7	−0.08	−0.8
11	17	41.2	7.4	0.41	3.8
12	8	25.0	5.3	−0.38	−3.2
13	2	0.0	8.3	−0.50	−3.7
Average		63.8	5.0		

Table 5

Statistics comparing reader/tester data for Atka mackerel in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
1	15	100.0	0.0	0.00	0.0
2	76	97.4	1.2	0.00	0.0
3	47	55.3	14.2	0.02	0.9
4	28	64.3	10.3	−0.11	−2.8
5	29	48.3	10.1	0.03	1.1
6	28	50.0	6.8	0.11	1.8
7	20	65.0	5.4	−0.40	−6.0
8	35	40.0	7.2	−0.26	−3.4
9	4	25.0	8.1	0.00	0.3
10	4	50.0	3.7	−0.50	−5.3
Average		66.8	6.8		

Table 6

Statistics comparing reader/tester data for sablefish in 1986. Bias is between-reader bias; nominal age is mean.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
1	13	100.0	0.0	0.00	0.0
2	43	88.4	5.5	0.02	1.6
3	43	58.1	13.4	−0.21	−7.8
4	24	58.3	10.1	−0.25	−7.1
5	49	53.1	10.2	0.51	10.8
6	50	34.0	12.7	0.82	14.4
7	29	37.9	12.1	0.79	11.7
8	17	11.8	15.0	1.18	15.2
9	21	0.0	20.6	2.33	26.9
10	11	0.0	24.2	3.00	30.3
11	11	9.1	17.4	1.73	16.0
12	12	8.3	24.1	3.83	32.7
13	5	0.0	29.9	5.40	42.3
14	4	0.0	36.7	4.50	33.3
15	1	0.0	4.9	1.00	6.9
16	1	0.0	31.9	7.00	45.2
18	2	0.0	8.1	1.00	5.7
19	2	0.0	35.5	9.50	50.2
23	1	0.0	15.7	−5.00	−22.2
29	2	50.0	1.2	0.50	1.8
Average		43.7	12.9		

Table 7

Statistics comparing reader/tester data by individual readers for pollock in 1986. Reader A is less experienced than reader B. Bias is between-reader bias; nominal age is tester age.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
Results for Reader A					
1	21	85.7	6.7	0.14	9.5
2	46	87.0	4.1	0.09	2.9
3	95	80.0	4.2	0.16	4.3
4	94	72.3	4.9	0.02	−0.3
5	76	69.7	4.2	0.09	1.2
6	59	62.7	4.8	0.07	0.5
7	63	38.1	7.5	−0.17	−3.5
8	122	44.3	6.0	−0.18	−3.0
9	30	26.7	10.0	−0.30	−5.0
10	5	0.0	7.4	−1.00	−10.5
11	3	0.0	6.7	−1.00	−9.5
12	5	20.0	12.5	−1.80	−17.6
13	1	0.0	11.8	−2.00	−16.7
14	1	0.0	10.9	−2.00	−15.4
Average		61.0	5.5		
Results for Reader B					
2	11	100.0	0.0	0.00	0.0
3	30	86.7	3.2	0.00	−0.8
4	57	80.7	3.3	0.05	0.7
5	34	76.5	4.0	0.06	0.4
6	44	79.5	2.8	0.00	−0.4
7	35	80.0	2.0	0.09	1.0
8	54	74.1	2.5	−0.02	−0.5
9	29	24.1	7.1	−0.28	−3.8
10	8	50.0	5.3	0.00	−0.6
11	14	50.0	6.0	−0.57	−6.0
12	3	33.3	3.9	0.00	−0.2
Average		72.4	3.4		

Because percentage agreement decreases with the age of fish (Tables 1–6), and age distributions vary greatly among different species and among samples of the same species, percentage agreement lends itself only to age-specific comparisons. This is illustrated above by Pacific ocean perch and sablefish which show a similar percentage agreement; however, Pacific ocean perch is much more "ageable" than sablefish, as reflected in the corresponding coefficients of variation.

Although percentage agreement and coefficient of variation both reflect the relative difficulty of ageing each species, only the coefficient of variation adjusts for the absolute age of the fish. Therefore, one might conclude that the easiest species to age are Pacific whiting (Table 1) and yellowfin sole (Table 2); and the medium–difficult species are Pacific ocean perch (Table 3) and walleye pollock (Table 4).

The most difficult species to age—species with unresolved criteria, or species for which readers needed further training—were Atka mackerel (Table 5) and sablefish (Table 6). In fact, in this study the age-reader for Atka mackerel was inexperienced with the species, and there were unresolved criteria for sablefish.

The most important usage of reader/tester data is in maintaining quality control. Unlike the data presented in Tables 1–6, for quality-control purposes we need to compare only one tester with one reader, with the nominal age being the tester age. For pollock (Table 7) there were significant between-reader biases at older ages in the case of inexperienced reader A. There were no such between-reader biases for the experienced reader B. To ensure data quality, these types of between-reader biases are constantly reviewed and the samples partially re-aged, before the data are released for use.

Sablefish is an especially difficult species to age (Table 8). There were so many problems with age determination that we suspended ageing, reviewed criteria with other ageing labs, and re-aged several large samples. It is probable that between-reader bias for this species can be reduced, but it is doubtful that the coefficient of variation for this species can be substantially reduced. Nevertheless, the availability of reader/tester data was useful in revealing problems. Also, data users deserve a quantitative presentation of variability in age determinations and may be able to use these

Table 8

Statistics comparing reader/tester data for individual Reader A ageing sablefish in 1986. Bias is between-reader bias; nominal age is tester age.

Age (yr)	Count	Percentage agreement	CV (%)	Bias (yr)	Percentage bias
1	16	81.3	8.8	0.19	12.5
2	47	80.9	7.3	0.19	4.6
3	40	62.5	10.9	−0.08	−6.6
4	41	34.1	14.7	0.68	12.5
5	62	41.9	14.1	0.82	10.0
6	40	42.5	12.2	1.05	12.7
7	29	37.9	11.9	1.28	14.6
8	23	8.7	21.6	2.83	24.2
9	15	0.0	21.4	2.87	23.7
10	6	0.0	14.4	1.67	13.3
11	8	12.5	15.6	2.88	17.2
12	6	16.7	13.3	1.17	6.4
14	1	0.0	4.9	1.00	6.9
16	2	0.0	19.2	−1.00	−9.9
17	1	0.0	11.5	3.00	16.2
18	1	0.0	4.0	−1.00	−5.7
25	1	0.0	15.7	−5.00	−22.2
28	1	0.0	2.5	1.00	3.5
29	1	100.0	0.0	0.00	0.0
Average		43.7	12.9		

data for making decisions on aspects of their data analysis and modeling.

We examined the question of consistency between the percentage agreement and coefficient of variation measures of variability when analyzing between-reader data. Earlier we showed that assuming a constant coefficient of variation, and the normal error model, the percentage agreement can be predicted for all nominal ages. By comparing these theoretical curves with estimated percentage agreements calculated from data (Tables 1–6), some confidence in the consistency of the two measures can be derived. However, this comparison is crude due to the probable existence of between-reader biases that are not factored into the analysis.

Four different values for the coefficients of variation were used to calculate theoretical percentage agreement curves (Fig. 1A). These curves were then compared with estimated percentage agreement values for yellowfin sole (CV = 0.032, Fig. 1B), walleye pollock (CV = 0.050, Fig. 1C), and sablefish (CV = 0.129, Fig. 1D).

The percentage agreements for all three species appear consistent with the hypothesis that the coefficient of variation is constant over a wide age range, although the percentage agreements for pollock are biased low. These results support averaging the coefficient of variation across age ranges, and generally support using the coefficient of variation for interpreting precision data from age-determination studies. However, there is considerable variation in these data which makes our results somewhat tentative.

An important factor that also affects the ageing process is the presence of a strong year-class. For example, if two adjacent year-classes have absolute strengths of 10 and 100 fish, a 10% imprecision of ±1 year will add 5 fish from the strong cohort to the weak one (a 50% change) but only one-half a fish from the weak year-class to the strong (a 0.5% change). The data on Pacific whiting (Table 1) show how this phenomenon can lead to poor percentage agreements for weaker year-classes.

Users of age data are often concerned that after some age, say 9 years, for example, the dominant year-classes become spread over several ages. Since percentage agreement by such an age has often decreased to 50% or less, it is expected that age distributions will be smoothed. The only reason the ages would not be smoothed is if the dominant year-class is being anticipated by the age-reader. For example, if samples are 90% 10-year-olds, it would be difficult for the age-reader not to anticipate that age and between-reader agreement would be high. However, if say 9-, 10-, and 11-year- olds occur in equal numbers, the agreement would not be nearly as good.

Two possible ways of handling this problem are evident. A controversial method would be to assure that all age-readers are reasonably coached as to the probable occurrence of a strong year-class; the other is to group the older ages in any model analyzing these data (e.g., Deriso et al. 1989). Both approaches avoid asking the age-reader to perform the impossible.

Finally, interpretation and analysis of repeated readings given here assume that the repeated readings were statistically independent. In the present context, this simply means that each reader did not have information regarding the other reader's results. When repeated readings are not made on an independent basis, or are of inadequate sample size, the data will be difficult or impossible to interpret statistically. From such a database, it is impossible to make assertions regarding precision.

Acknowledgments

Mr. George Hirschhorn had the foresight to initiate the reader/tester quality control system. We thank the age readers of the Ageing Unit at the Alaska Fisheries Science Center who provided the data for this study. We also thank the Scientific Editor and three anonymous referees whose comments contributed significantly to this paper.

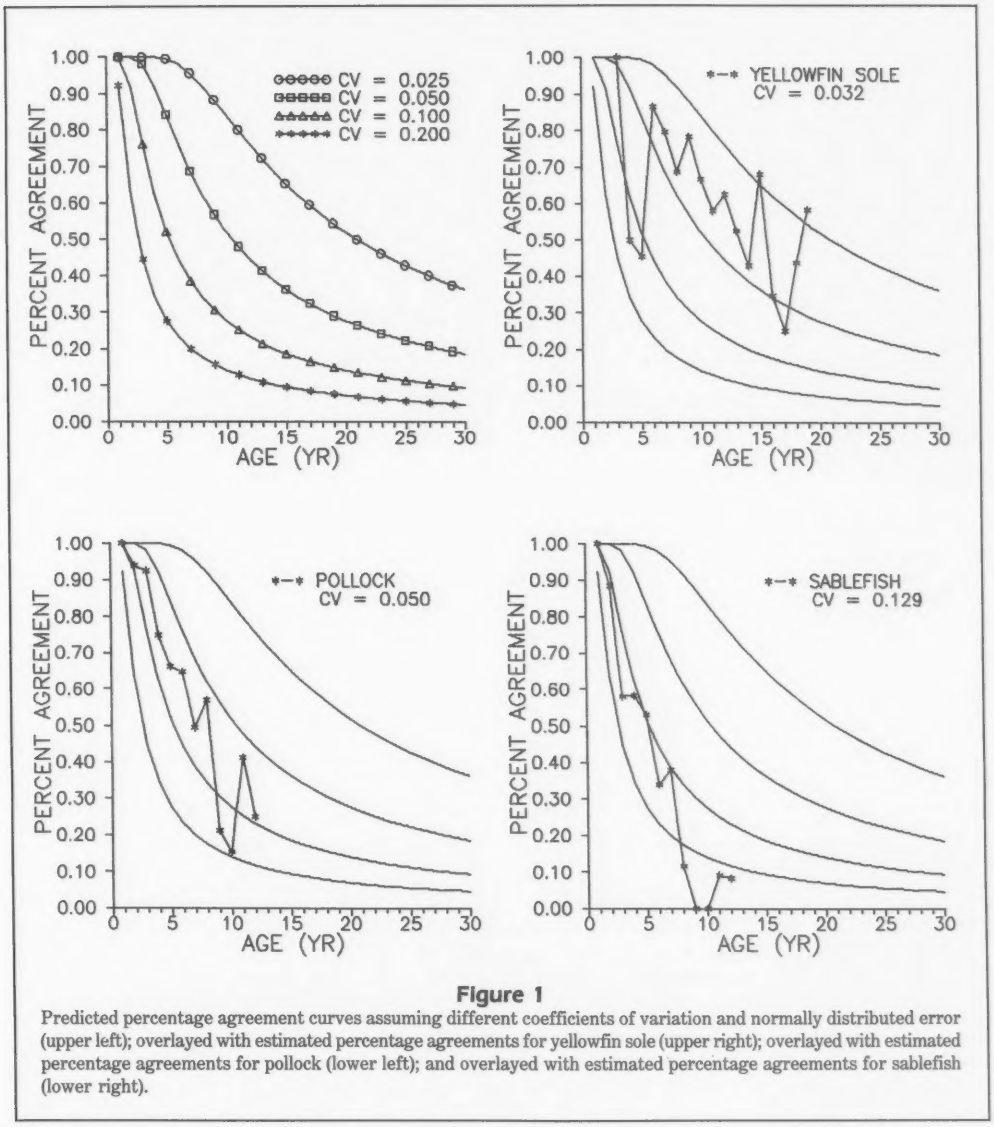


Figure 1

Predicted percentage agreement curves assuming different coefficients of variation and normally distributed error (upper left); overlayed with estimated percentage agreements for yellowfin sole (upper right); overlayed with estimated percentage agreements for pollock (lower left); and overlayed with estimated percentage agreements for sablefish (lower right).

Citations

Beamish, R.J., and D.A. Fournier
1981 A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982–983.

Beamish, R.J., and G.A. McFarlane
1983 The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743.
1987 Current trends in age determination methodology. *In* Summerfelt, R.C., and G.E. Hall (eds.), Age and growth of fish, p. 15–42. Iowa State Univ. Press, Ames.

Beamish, R.J., G.A. McFarlane, and D.E. Chilton
1983 Use of oxytetracycline and other methods to validate a method of age determination for sablefish (*Anoplopoma fimbria*). *In* Proceedings of the international sablefish symposium, p. 95–116. Alaska Sea Grant Rep. 83-8, Univ. Alaska, Fairbanks.

Bennett, J.T., G.W. Boehlert, and K.K. Turekian
1982 Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) from Ra-226/Pb-210 measurements in otoliths. Mar. Biol. (Berl.) 71:209–215.

Campana, S.E., K.C.T. Zwanenburg, and J.N. Smith
1990 $^{210}Pb/^{226}Ra$ determination of longevity in redfish. Can. J. Fish. Aquat. Sci. 47:163–165.

Cass, A.J., and R.J. Beamish
1983 First evidence of validity of the fin-ray method of age

determination for marine fishes. N. Am. J. Fish. Manage. 3:182–188.

Chang, W.Y.B.
1982 A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39:1208–1210.

Chilton, D.E., and R.J. Beamish
1982 Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Can. Spec. Publ. Fish. Aquat. Sci. 60, 102 p.

Deriso, R.B., T.J. Quinn II, and P.R. Neal
1989 Further aspects of catch-age analysis with auxiliary information. *In* Beamish, R.J., and G.A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment, p. 127–135. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Kimura, D.K., R.R. Mandapat, and S.L. Oxford
1979 Method, validity, and variability in the age determination of yellowtail rockfish (*Sebastes flavidus*), using otoliths. J. Fish. Res. Board Can. 36:377–383.

Leaman, B.M., and D.A. Nagtegaal
1987 Age validation and revised natural mortality rate for yellowtail rockfish. Trans. Am. Fish. Soc. 116:171–175.

McFarlane, G.A., and R.J. Beamish
1987 Validation of the dorsal spine method of age determination for spiny dogfish. *In* Summerfelt, R.C., and G.E. Hall (eds.), Age and growth of fish, p. 287–300. Iowa State Univ. Press, Ames.

Theobald, C.M., and J.R. Mallinson
1978 Comparative calibration, linear structural relationships and congeneric measurements. Biometrics 34:39–45.

Survival and Growth of Early-Juvenile American Lobsters *Homarus americanus* Through Their First Season While Fed Diets of Mesoplankton, Microplankton, and Frozen Brine Shrimp

Kari L. Lavalli

Boston University Marine Program, Marine Biological Laboratory
Woods Hole, Massachusetts 02543

Abstract.– Early juvenile (Stages V–IX) American lobsters *Homarus americanus* were fed diets of mesoplankton in filtered seawater, meso/microplankton combination in filtered seawater, and frozen brine shrimp in both filtered and unfiltered seawater to determine if mesoplankton diets could sustain survival and growth throughout most of the first year of molts and if smaller zooplankters and phytoplankton in the meso/microplankton diet could be utilized as food and could sustain survival in periods of low food supply. At the beginning of the experiment, there were no significant differences in either carapace length or weight between the groups of sibling lobsters. Lobsters fed mesoplankton had high survival (80%) and significant increases in both carapace length and weight, although they weighed less at Stage IX than those fed frozen brine shrimp in unfiltered seawater. Lobsters fed frozen brine shrimp in filtered seawater had low survival (15%), but did not differ significantly at Stage IX from those fed mesoplankton in terms of both carapace length and weight. Lobsters fed brine shrimp in unfiltered seawater had high survival rates (95%) and weighed nearly twice as much at Stage IX than both the brine shrimp-fed lobsters in filtered seawater and the mesoplankton-fed lobsters; however, none of these three surviving groups differed significantly in carapace length at Stage IX. Intermolt periods for the three surviving groups were not significantly different until the molt between Stage VIII and IX when the mesoplankton-fed lobsters took nearly twice as long to molt as either of the brine shrimp-fed groups. Lobsters fed meso/microplankton did not molt out of Stage V and died within 36 days of the 107-day experiment. These results indicate that mesoplankton diets promote growth and survival of lobsters throughout most of their first season of molting and that larger planktonic organisms may contain essential nutritional requirements not met by brine shrimp alone. However, the meso/microplankton diet, consisting mostly of diatoms, does not provide sufficient nutrition for survival during periods of starvation.

Manuscript accepted 6 August 1990.
Fishery Bulletin, U.S. 89:61–68 (1991).

Little is known of the natural foraging activities of the settled postlarvae (Stage IV) and early-juvenile (<1 year-old) stages of the American lobster *Homarus americanus*, presumably due to the inability of past investigators to locate them in the benthic environment. Recently, Barshaw and Bryant-Rich (1988) examined the behavior of the early-juvenile American lobster in naturalistic settings in the laboratory and found that they spent a considerable amount of time pleopod fanning (15% of the time) and antennule flicking (15–40% of the time) at the entrance of their burrows. During their 8-month investigation, Barshaw and Bryant-Rich never observed an early-juvenile lobster leave its burrow; of the several instances where lobsters were seen feeding, they captured amphipods near the entrance of the burrow twice while other observations indicated that the lobsters were capturing planktonic organisms via self-generated currents which drew the organisms toward the burrow entrance. Their observations are corroborated by field cage studies of Gregory Roach (Nova Scotia Dep. Fish., Halifax, N.S., Canada B3J 3C4, pers. commun., Nov. 1989) where he, too, never observed early-juvenile American lobsters leave their burrows during one year of observations.

While little is known about the natural diet of recently settled American lobsters, Cobb et al. (1983) observed presettlement Stage-IV American lobsters capturing crab megalopae and insects in the field. Stomach content analyses indicate that the Stage-IV diet is similar to that of the larvae, consisting of copepods, decapod larvae, amphipods, algae, and diatoms (Williams 1907, Herrick 1911, Templeman and Tibbo 1945). Although most laboratory investigations have used artificial feeds which wild early-juvenile lobsters would never encounter, some studies have provided information on naturalistic diets. Emmel (1908) found that Stage-IV American lobsters were capable of surviving on planktonic organisms obtained from the water alone. The intermolt period for this group of lobsters was significantly longer than that for groups fed on beef, soft-shelled clam, lobster muscle, or shredded fish, but this result was probably due to differences in the overall amount of food available to the groups, as unequal weights of food were used. More recently, Andrea (1975), D'Agostino (1980), and Good et al. (1982) found that when amphipods were used as a food source, growth rates of larval, post-larval, and early-juvenile American lobsters improved significantly over brine shrimp diets (both live and

frozen) and artificially prepared compound diets. Daniel et al. (1985) demonstrated that Stage-IV and early-juvenile American lobsters were capable of surviving and growing on a frozen filtrate diet consisting of 99% barnacle larvae and 1% calanoid copepods; however, these filtrate-fed lobsters were significantly smaller (by 17%) than lobsters fed on frozen adult brine shrimp. Similarly, Barshaw (1989) found that Stage-IV American lobsters were also capable of surviving and growing through two molts on a diet of live, unidentified plankton (size 152–1000 μm), although the plankton-fed lobsters were smaller and had a greater intermolt period from Stage V to VI than those fed on frozen brine shrimp. In all of the above studies, there were no differences in mortality between the different groups of fed lobsters.

This study examined the survival and growth of early-juvenile (Stages V–IX) American lobsters fed on diets of mesoplankton (95–1000 μm) and a meso/microplankton combination (25–95 μm) while using frozen brine shrimp diets for reference. Studies with other crustaceans indicate that phytoplankton may be used as a supplement when zooplankton abundance is low and its presence may extend the period of survival over that observed for starved animals (McConaugha 1985). However, the nutritional value of phytoplankton is highly dependent on its content of essential fatty acids which can vary in response to temperature, dissolved nutrients, light, and age (Castell and Kean 1986). While American lobsters have not been classified as algal feeders (Lebour 1922), stomach content analyses of the larvae and postlarvae indicate that diatoms and other algae form part of their diet (Herrick 1895, Williams 1907, Herrick 1911). Recently, Lavalli and Barshaw (1989) have shown that Stage-IV and -V American lobsters are capable of removing particles from the water column to at least a size of 70 μm, indicating that early-juvenile lobsters may be able to utilize small organisms in the mesoplankton and microplankton. This study was designed, in particular, to determine two things: (1) Whether early juveniles could utilize an already-proven diet (mesoplankton) for Stage-IV and -V lobsters throughout much of their first season of molting activity, and (2) whether early juveniles could extend survival by utilizing the organisms found in the smaller range of mesoplankton and in the microplankton.

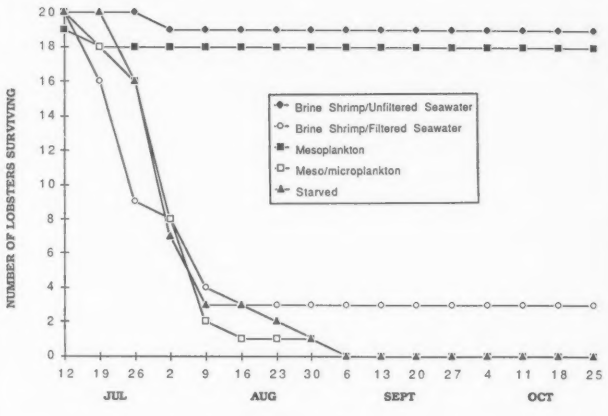


Figure 1

Mean number of original 20 lobsters surviving through the 107 days of the experiment (molt stages V–IX) on each of the diet regimes: brine shrimp in unfiltered seawater, brine shrimp in filtered seawater, mesoplankton (95–1000 μm) in filtered seawater, meso/microplankton combination (25–95 μm) in filtered seawater, and starved.

Materials and methods

Prior to the beginning of the experiment, Stage-IV American lobster siblings *Homarus americanus* were held collectively in a seawater table supplied with ambient, unfiltered seawater and were fed *ad libitum* on frozen adult *Artemia* (San Francisco Bay type). Siblings were used for the experiment, since genetic differences between females can produce significant differences in weight among similarly raised juvenile lobsters (Conklin et al. 1975, Hedgecock and Nelson 1978). The lobsters were then randomly assigned to one of four groups of 20 animals: a mesoplankton-fed group (95–1000 μm), a meso/microplankton combination-fed group (25–95 μm), a frozen brine shrimp-fed group, and a starved group. Upon assignment, individual lobsters were placed into plastic trays (Rubbermaid Drawer Organizers, No. 2915) with dimensions 224 mm long × 75 mm wide × 50 mm deep, and volume of ~750 mL. Each tray was modified to include a sidewall screen for water flow and a dark-grey PVC tube (10 mm diameter) glued to the bottom which could act as a shelter. The trays were provided with ambient seawater which was filtered with a dual-cartridge filtering system (a 50-μm honeycomb filter followed by a 5-μm nominal filter). They were arranged in a Latin square design to intersperse the treatments and were kept in darkness, except during cleaning and feeding periods, as previous investigations demonstrated that juvenile lobsters

grew more quickly and were more active in a nearly constant dark regime (Bordner and Conklin 1981). The water flow to the trays was turned off for 1 hour after the introduction of food to allow the lobsters to more easily capture the food. Filters were replaced during these feeding periods if they were clogged.

Lobsters were fed according to group; excess food and other debris were removed daily with a kitchen baster. All trays were thoroughly scrubbed each week to remove algal growth from the sidewalls and bottom. During cleaning the lobsters were held in a moist, small-mesh fish net. Every attempt was made to feed equal wet weights of food, and representative portions of each diet were weighed each week. For the plankton diets, representative portions were also photographed using the technique of silhouette photography (Edgerton 1977, Ortner et al. 1979) so that identification of the planktonic organisms could be made without the aid of a microscope.

Plankton was collected three to four times per week by towing with a #10 plankton net (152 μm) and a phytoplankton net (25 μm) in the Waquoit Bay/Nantucket Sound areas. After collection it was sieved to remove objects >1000 μm and to divide the plankton into each size group. Half of the plankton was used immediately while the other half was refrigerated overnight and used the following day.

Carapace lengths of Stage-V lobsters were measured to the nearest 0.1 mm using calipers, and their weights were recorded on a Brainweigh B300D scale to the nearest 0.001 g. The lobsters were blotted with absorbent paper to remove excess water prior to weighing. The experiment ran until all surviving lobsters attained Stage IX. During this time, the dates for all molts (for the determination of intermolt periods) and deaths were recorded. Although no post-mortems were performed, it was noted whether lobsters died in the process of molting or of unknown causes. Coloration of the lobsters was also noted. After achieving Stage IX, the lobsters were once again measured and weighed.

During the time of this experiment, a fifth group of lobsters (also siblings of the other four groups of lobsters) was raised in seawater tables for another experiment. The lobsters in this fifth group were placed individually into separate circular containers (85 mm diameter; 200 mm high) consisting of a black plastic bottom glued to a cylinder made of screening (1-mm mesh). These lobsters were fed the same amount of brine shrimp as the brine shrimp group of lobsters above, but lived in unfiltered, ambient seawater and were subject to ambient daylight plus overhead fluorescent lighting. Organic debris was cleaned out of the seawater table and containers at least once per month. While data on the initial (Stage V) weights and carapace lengths are unavailable for this fifth group of lobsters, their final (Stage IX) weight and carapace length were recorded. Intermolt periods were recorded except for the period between Stages V and VI, since this group was held communally until after they had molted into Stage V.

Data for each of the measurements taken (intermolt period, initial (Stage V) and final (Stage IX) carapace lengths and weights) were analyzed using the Student's t-test when comparisons between two groups or two measurements within a group (i.e., initial and final weights or carapace lengths) were made, and by 1-way ANOVA tests when more than two groups were compared. Where ANOVA tests indicated significant differences were present, the groups were compared to determine which groups were different by using the Tukey test with unequal sample sizes. Differences in survival rates were tested with a 2×2 chi-square contingency table. This experiment was conducted at the Marine Biological Laboratory in Woods Hole, MA from 13 July to 27 October 1987. The ambient seawater temperature ranged from 23 to 14.5°C and averaged 19.6°C.

Results

Survival was high in the groups fed brine shrimp in unfiltered seawater (95% survival), brine shrimp in filtered seawater (95% survival), and mesoplankton (90% survival) for the molt between Stage V and VI. During the subsequent molts, however, the group fed brine shrimp in filtered seawater had significantly higher mortality (χ^2, $P<0.001$; Fig. 1), with only 15% survival by the end of the experiment. The survival of the brine shrimp-fed group in unfiltered seawater remained unchanged, while that of the mesoplankton-fed group fell to 80% by the end of the experiment. However, there was no significant difference in survival between these two groups. Of the deaths noted for each of the groups, one lobster fed brine shrimp in unfiltered seawater and one fed mesoplankton died during its molt; of the 17 lobsters which died on the brine shrimp diet in filtered seawater, 14 died while in the process of molting. Coloration of the surviving groups differed, with the brine shrimp-fed group in filtered seawater being pale blue, typical of brine shrimp-fed lobsters, and the mesoplankton-fed group and brine shrimp-fed group in unfiltered seawater being the wild-type coloration.

None of the starved or meso/microplankton combination-fed lobsters molted beyond Stage V. All of the lobsters in these two groups died within 36 days of the 107-day experiment, and although the lobsters fed the meso/microplankton combination diet took slightly

longer to die (23.842 ± 10.035 (SD) days vs. 21.75 ± 7.063 days), this difference was not significant.

Intermolt duration data (Fig. 2) showed that the brine shrimp-fed group in filtered seawater took significantly longer to molt (by 1 day) into Stage VI than the mesoplankton-fed group (10.412 ± 1.502 days vs. 11.389 ± 1.243 days; Student's t-test, $P<0.025$). Data are not available on the intermolt period between Stages V and VI for the brine shrimp-fed group in unfiltered seawater. There was no significant difference between the groups brine shrimp-fed in filtered seawater, brine shrimp-fed in unfiltered seawater, and mesoplankton-fed for the intermolt periods between Stages VI and VII (14.857 ± 2.035 vs. 13.444 ± 1.653 vs. 14.059 ± 1.853 days) and Stages VII and VIII (22.0 ± 7.810 vs. 20.556 ± 4.681 vs. 20.529 ± 2.528 days). However, the intermolt periods of both brine shrimp-fed groups were significantly different (18.0 ± 1 and 16.842 ± 2.292 days; 1-way ANOVA, $P<0.001$; Tukey test, $P<0.001$) from those of the mesoplankton-fed group (36 ± 5.057 days) for the molt between Stages VIII and IX, with the two brine shrimp-fed groups taking nearly half the time of the mesoplankton-fed group to molt into Stage IX.

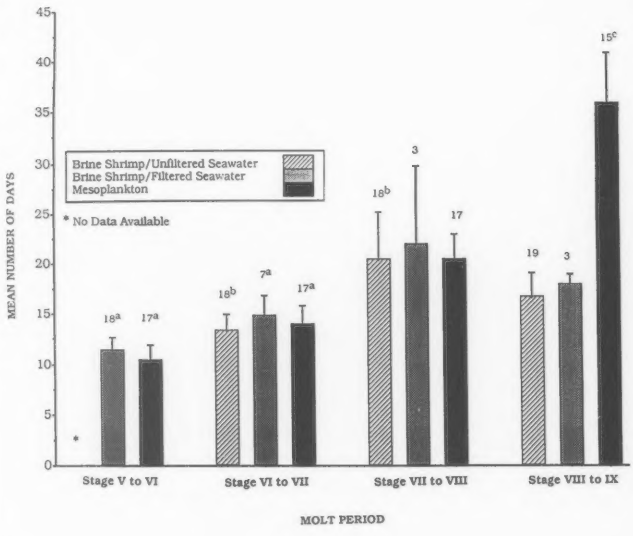


Figure 2

Mean intermolt durations for lobsters on each of three diet regimes: brine shrimp in unfiltered seawater, brine shrimp in filtered seawater, and mesoplankton (95–1000 μm) in filtered seawater. Bars indicate standard deviation values. ([a]) Stage VI molt date missed for one lobster, so intermolt period could not be determined for Stages V–VI and VI–VII for that lobster. ([b]) Stage VII molt date missed for one lobster, so intermolt period could not be determined for Stages VI–VII and VII–VIII for that lobster. ([c]) Stage IX molt date missed for one lobster, so intermolt period could not be determined for Stages VIII–IX for that lobster.

There was no significant difference between any of the groups brine shrimp-fed in filtered seawater, mesoplankton-fed, meso/microplankton combination-fed, and starved lobsters at the beginning of the experiment in either weight (0.06 ± 0.011 vs. 0.066 ± 0.011 vs. 0.059 ± 0.009 vs. 0.061 ± 0.011 g, respectively; Fig. 3) or carapace length (4.66 ± 0.214 vs. 4.761 ± 0.214 vs. 4.739 ± 0.236 vs. 4.716 ± 0.236 mm respectively; Fig. 4). Although measurements are not available for the brine shrimp-fed group in unfiltered seawater, they probably did not differ significantly from the other groups since they were maintained in conditions identical to their siblings until immediately before the molt to Stage V. Each of the surviving groups of lobsters fed brine shrimp in filtered seawater, brine shrimp in unfiltered seawater, and mesoplankton showed significant growth (Student's t-test, $P<0.001$) in terms of both increased weight and carapace length (Figs. 3 and 4). However, final (Stage IX) weights did differ between groups (1-way ANOVA, $P<0.001$). The weight of the brine shrimp-fed group in unfiltered seawater (0.837 ± 0.117 g) was significantly greater (Tukey test, $P<0.001$) than that of both the brine shrimp-fed group in filtered seawater (0.484 ± 0.183 g) and the mesoplankton-fed group (0.484 ± 0.037 g). However, there was no significant difference between the latter two groups. Final (Stage IX) carapace lengths did not differ between the three surviving groups (brine shrimp-fed in filtered seawater, 9.9 ± 1.353 mm; brine shrimp-fed in unfiltered seawater, 10.459 ± 0.564 mm; mesoplankton-fed, 9.907 ± 0.732 mm).

There was no significant difference in the wet weights of each diet fed the lobsters. The average wet weights of the diets were 0.408 ± 0.095 g for the mesoplankton; 0.364 ± 0.108 g for the meso/microplankton combination diet; and 0.391 ± 0.072 g for the brine shrimp diets. The mesoplankton diet consisted predominantly of *Acartia* copepods, barnacle nauplii, pagurid shrimp zoea, invertebrate eggs, brachyuran crab zoea, foraminifera, centric and pennate diatoms, and marine algae, with occasional instances of ascidian tadpoles, barnacle exoskeletons, fish eggs and young, amphipods, hydroids, brachyuran crab prezoea,

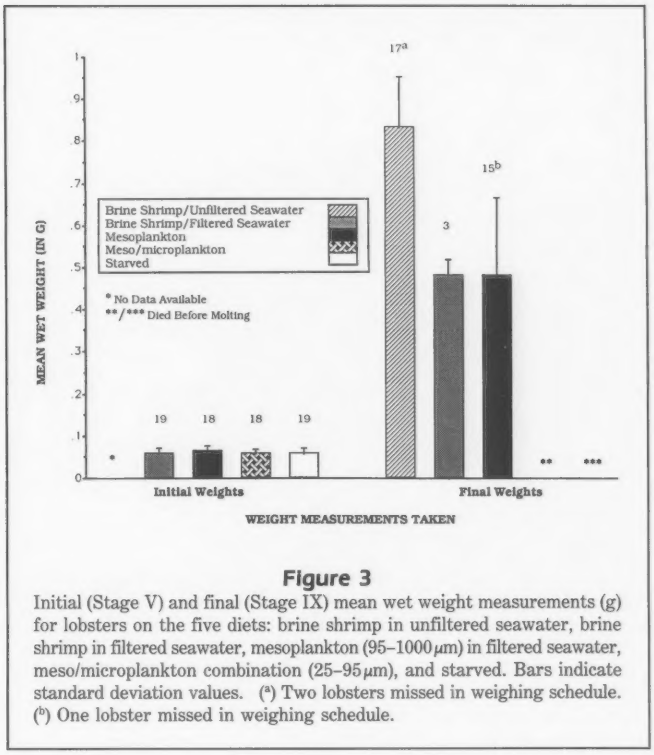


Figure 3

Initial (Stage V) and final (Stage IX) mean wet weight measurements (g) for lobsters on the five diets: brine shrimp in unfiltered seawater, brine shrimp in filtered seawater, mesoplankton (95–1000 μm) in filtered seawater, meso/microplankton combination (25–95 μm), and starved. Bars indicate standard deviation values. (a) Two lobsters missed in weighing schedule. (b) One lobster missed in weighing schedule.

caridean shrimp zoea, *Centropages* and *Calanus* copepods, dinoflagellates, and juvenile nemertea. The meso/microplankton combination diet typically consisted of centric and pennate diatoms with occasional instances of fragments of marine algae and crustaceans.

Discussion

The results clearly indicate that early juvenile American lobsters are not capable of extending survival on a diet consisting mostly of diatoms, despite their common presence in stomach content analyses (Herrick 1895, Williams 1907, Herrick 1911). Larger planktonic organisms are required for survival and growth. This result is not entirely surprising even though Lavalli and Barshaw (1989) showed that post-larval and early juvenile (Stage V) American lobsters could remove particles from the water down to a size of at least 70 μm. Other crustaceans fed on phytoplankton can gain some nutrients and extend their survival in periods of low

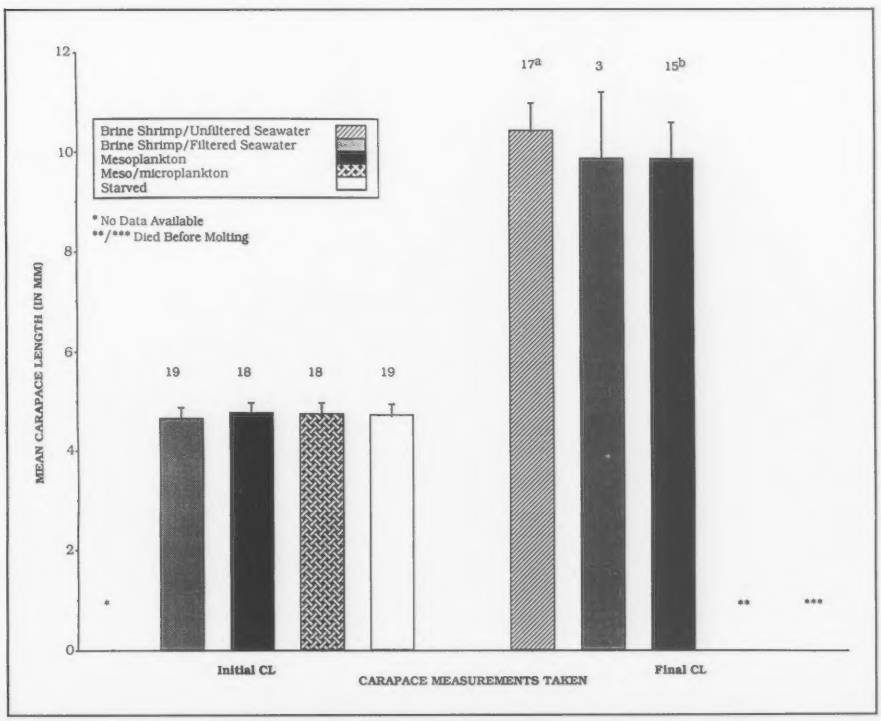


Figure 4

Initial (Stage V) and final (Stage IX) mean carapace length measurements (mm) for lobsters on the five diets: brine shrimp in unfiltered seawater, brine shrimp in filtered seawater, mesoplankton (95–1000 μm) in filtered seawater, meso/microplankton combination, and starved. Bars indicate standard deviation values. (a) Two lobsters missed in carapace-length measuring schedule. (b) One lobster missed in carapace-length measuring schedule.

food abundance, but this type of diet does not support molting or growth (McConaugha 1985). Post-larval lobsters are known to contain diatoms and other algae in their guts (Herrick 1895, Williams 1907, Herrick 1911) which suggests some nutritional role for these items, but one not fully understood nor clarified by this experiment. The smaller planktonic organisms in the meso/microplankton combination diet may not have been present in sufficient numbers to make up for the small amount of nutrients derived. Because the meso/microplankton diet consisted mostly of diatoms which have a high content of silicon-based ash, it is likely that this diet had a greater percentage of non-digestible fiber or bulk than that in the mesoplankton or brine shrimp diets (John Castell, Dep. Fish. & Oceans, Halifax, N.S., Canada B3J 2S7, pers. commun., May 1990). Furthermore, these smaller organisms may have been more easily flushed out of the containers when the water flow resumed.

The results presented here also clearly support those of Barshaw (1989) and Daniel et al. (1985) in terms of postlarval and early-juvenile lobsters being capable of surviving on mesoplankton, and in demonstrating high survival among the brine shrimp-fed (in filtered seawater) and mesoplankton-fed groups through Stage VI. These studies differ, however, in that Barshaw (1989) found molt delays in her plankton-fed group between Stages V and VI, whereas no molt delays were found in this study until Stage VIII. Barshaw's lobsters also took longer to molt into Stage VI (34 days for the plankton-fed lobsters and 23 days for the brine shrimp-fed lobsters) than did the lobsters in this experiment (10 and 11 days for the same groups), indicating that they were not receiving enough food and thus took longer to build up the reserves to molt. In addition, both Daniel et al. (1985) and Barshaw (1989) found that lobsters fed on frozen brine shrimp in filtered seawater were significantly larger than the filtrate-fed or plankton-fed lobsters. This study found no such difference between the similarly treated groups.

The differences between the two groups of lobsters fed on brine shrimp diets were striking. Lobsters fed brine shrimp in the filtered seawater had pale blue coloration and poor survival, with the majority of deaths occurring during molting. However, this difference in survival was not present until after Stage VI where Barshaw's (1989) experiment ended. Similar drops in survival of brine shrimp-fed lobsters in filtered seawater after Stage VI have been observed by Colleen Boggs (Edgerton Res. Lab. [in collaboration with the Kravitz Lab., Harvard Medical School], New England Aquarium, Boston 02110, pers. commun., summer 1990). Certain strains of brine shrimp promote better growth than others (McConaugha 1985), and the success of one strain versus another is linked to its fatty acid content (Fujita et al. 1980), the presence of which is extremely important for the survival of postlarval and early-juvenile American lobsters (D'Abramo et al. 1981). The San Francisco Bay brand used in this experiment is intermediate in lipid content (McConaugha 1985), but even different lots of the same strain of brine shrimp are known to be highly variable in quality (Eagles et al. 1984, 1986). Thus, whatever nutritional component was lacking in the lot of the brine shrimp used in this experiment was compensated by the planktonic organisms entering through the ambient water supply, since the brine shrimp-fed group of lobsters in unfiltered seawater showed high survival, a greater weight increase compared with those in filtered seawater, and wild-type coloration. What is particularly interesting, though, is that while the lobsters fed brine shrimp in unfiltered seawater were nearly twice as heavy at Stage IX as both those fed brine shrimp in filtered seawater and mesoplankton, there was no significant difference at Stage IX between any of these groups in terms of carapace lengths. Weight, therefore, might be a more important index of growth in early-juvenile lobsters. The carapace lengths achieved by the three surviving groups of lobsters at Stage IX were shorter than those predicted by calculations of Hudon (1987) from early juveniles captured in the field. This contradiction may have resulted from the lobsters used in this experiment being hatchery- and laboratory-reared and thus being typically smaller than wild lobsters at Stage V (pers. observ.).

The difference in weights at Stage IX between lobsters fed brine shrimp in unfiltered seawater and those fed mesoplankton indicates that growth (as well as survival) might be significantly enhanced if the lobsters have access to both a planktonic diet and a diet of small benthic organisms. Andrea (1975) demonstrated that lobster larvae (Stages I–IV) fed frozen copepods or frozen amphipods had significantly higher survival rates than those fed frozen brine shrimp. Furthermore, those larvae fed live copepods had higher survival than those fed both live and frozen adult brine shrimp when held under the same rearing conditions. Andrea's data also showed that the increase in carapace length and the gain in weight by lobsters fed diets of live copepods were comparable to the increases found in lobsters fed live brine shrimp.

Evidence to date indicates that early juveniles are found in shallow subtidal areas (Cooper and Uzmann 1980, Hudon 1987, Able et al. 1988, Wahle 1990) where they would have access to suprabenthic plankton and epiplankton (Wieser 1960, Cornet et al. 1983) as well as surface plankton that vertically migrate in response to light/dark conditions (Hardy 1970). They would also have access to the many benthic organisms found in subtidal areas (Orth 1973, Reise 1977). In support of

this hypothesis, postlarvae and early juveniles in laboratory settings have been observed to lunge out of their burrows to grab at food (amphipods) passing by (Berrill 1974 with *H. gammarus*; Barshaw and Bryant-Rich 1988) or to stalk swimming amphipods (Good et al. 1982). Also, Crnkovic (1968) suggested that the creation of new openings in existing *Nephrops norvegicus* burrows may be linked to searching for food within the sediment.

The intermolt periods, with the exception of that for the mesoplankton-fed group between Stages VIII and IX, were consistent with or shorter than previous studies at the same average temperature (19°C) (Templeman 1948, as reported in Wilder 1953) and were close to the values predicted by Hudon (1987) for the same stages. These results show that early-juvenile lobsters fed on mesoplankton are able to capture it effectively enough to keep pace with the brine shrimp-fed lobsters in terms of intermolt periods until Stage VIII. At that time, the mesoplankton-fed lobsters spend nearly twice as much time in intermolt than either of the brine shrimp-fed groups. This result could be indicative of one of three conditions or some combination of all of them: (1) Either the lobsters became less efficient at capturing the plankton, (2) the planktonic organisms were not present in sufficient numbers in this study to compete with a brine shrimp diet at later stages, or (3) dietary requirements change with later molt stages.

In support of the first hypothesis is the fact that the claws of the postlarvae are small and symmetrical prior to Stage VIII. The claws slowly develop into the crusher and seizer claws during the early-juvenile stages; concomitant with this gradual development is a change in the posture of the lobster from one that is completely defensive (withdrawing or tail-flipping) to one that is more aggressive (Lang et al. 1977), and a change in the muscle fiber pattern and innervation of the two types of claws (Govind 1984). At Stage VIII the claw asymmetry is well established and the fiber composition and innervation are nearly the same as that found in the adult (Govind and Pearce 1986). These changes may indicate a shift in the feeding strategies used by the lobster, where capture of small benthic organisms becomes more important than the capture of planktonic organisms at or near Stage VIII.

As for the second hypothesis, Bordner and Conklin (1981) determined that older juvenile lobsters could consume up to 10% of their body weight per day. During this entire experiment, each group of lobsters was fed more than 10% of their body weight per day. Therefore, it seems unlikely that the later stages of lobsters were underfed on the mesoplankton diet. Finally, dietary requirements might indeed change as the lobster becomes more able to defend itself and thereby forage, and as the claws develop the ability to crush small molluscs; however, this experiment was not designed to answer such a question.

In conclusion, the results from this experiment contradict those of Barshaw (1989) and Daniel et al. (1985) in that they show no difference in growth and survival of early-juvenile lobsters (Stages V and VI) fed on a diet of mesoplankton versus a diet of frozen brine shrimp in filtered seawater. Stage VI–VIII lobsters are able to survive and grow on planktonic diets, but after Stage VIII they experience molt delays when compared with lobsters fed frozen brine shrimp diets. Despite this delay, the mesoplankton diet allows the early juveniles the opportunity to reach the predicted (Hudon 1987) winter stages of Stage VI (for late-fall settlers) to IX or X (for August settlers) without the need for other benthic food. Diets composed of smaller members of the mesoplankton plus microplankton do not provide sufficient nutrition to support survival in periods of low food abundance.

Acknowledgments

I thank Mike Syslo and Kevin Johnson of the Massachusetts State Lobster Hatchery for supplying me with Stage IV lobsters, and Dr. Harold Edgerton for instruction in the technique of silhouette photography. I also would like to thank Dr. Joe Costa (formerly of BUMP) for getting the boat up and running, and Paula Dolan (formerly of University of Tampa), Leslie Sammon (formerly of Mt. Holyoke College), and Lee Kefauver for their help in running the experiments and their willingness to go on plankton tows during the early hours of the morning in rain or shine. Drs. Jelle Atema, Stanley Cobb, Diana Barshaw, John Castell, and three anonymous reviewers provided helpful comments on the manuscript for which I am grateful.

Citations

Able, K.W., K.L. Heck, M.P. Fahay, and C.T. Roman
1988 Use of salt-marsh peat reefs by small juvenile lobsters on Cape Cod, Massachusetts. Estuaries 11:83–86.

Andrea, J.J.
1975 The nutritional adequacy and acceptability of several natural prey species for larval *Homarus americanus* (Milne-Edwards) in culture. M.S. thesis, Mar. Sci. Res. Cent., State Univ. New York, Stony Brook, 53 p.

Barshaw, D.E.
1989 Growth and survival of post-larval lobsters, *Homarus americanus*, on a diet of plankton. Fish. Bull., U.S. 87: 366–370.

Barshaw, D.E., and D.R. Bryant-Rich
1988 Long-term survival and behavior of early juvenile lobsters, *Homarus americanus*, in the three naturalistic substrates: Mud, rock, and eelgrass. Fish. Bull., U.S. 86:789–796.

Berrill, M.
1974 The burrowing behavior of newly-settled lobsters, *Homarus vulgaris* (Crustacea-Decapoda). J. Mar. Biol. Assoc. U.K. 54:797–801.

Bordner, C.E., and D.E. Conklin
1981 Food consumption and growth of juvenile lobsters. Aquaculture 24:285–300.

Castell, J.D., and J.C. Kean
1986 Evaluation of the role of nutrition in lobster recruitment. Can. J. Fish. Aquat. Sci. 43:2320–2327.

Cobb, J.S., T. Gulbransen, B.F. Phillips, D. Wang, and M. Syslo
1983 Behavior and distribution of larval and early juvenile *Homarus americanus*. Can. J. Fish. Aquat. Sci. 40:2184–2188.

Conklin, D.E., K. Devers, and R.A. Shleser
1975 Initial development of artificial diets for the lobster, *Homarus americanus*. Proc. World Maricult. Soc. 6:237–248.

Cooper, R.A., and J.R. Uzmann
1980 Ecology of juvenile and adult *Homarus*. *In* Cobb, J.S., and B.F. Phillips (eds.), The biology and management of lobsters, vol. II, p. 97–142. Academic Press, NY.

Cornet, M., J. Bouchet, J. Lissalde, J. Sorbe, and L. Amoureux
1983 Donnees qualitatives sur le benthos et le suprabenthos d'un transect du plateau continental sud-gascogne. Cah. Biol. Mar. 24:69–84 [in French, Engl. abstr.].

Crnkovic, D.
1968 Some observations regarding the burrows of juvenile *Nephrops norvegicus* (L.). Rapp. Comm. Int. Mer Medit. 19: 171–172.

D'Abramo, L.R., C.E. Bordner, D.E. Conklin, and N.A. Baum
1981 Essentiality of dietary phosphatidycholine for the survival of juvenile lobsters. J. Nutr. 111:425–431.

D'Agostino, A.
1980 Growth and color of juvenile lobsters (*Homarus americanus*) kept on diets of natural and artificial foodstuffs. *In* Proc., 1980 lobster nutrition workshop, p. 41–45. Maine Sea Grant Tech. Rep. 58, Univ. Maine, Orono.

Daniel, P.C., R.C. Bayer, and S. Chapman
1985 Barnacle larvae (*Balanus* spp.) as a potential diet for juvenile lobsters (*Homarus americanus*). Aquaculture 46:67–70.

Eagles, M.D., D.E. Aiken, and S.L. Waddy
1984 Effect of food quality and feeding schedule on survival, growth and development of larval American lobsters fed frozen adult brine shrimp. J. World Maricult. Soc. 15:142–143.
1986 Influence of light and food on larval American lobsters, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43:2303–2310.

Edgerton, H.E.
1977 Silhouette photography of small active subjects. J. Microsc. (Oxf.) 110:79–81.

Emmel, V.E.
1908 The problem of feeding methods in lobster culture. Annu. Rep. R.I. Comm. Inland Fish. 38:98–114 [avail. NMFS Woods Hole Lab., Woods Hole, MA 02543].

Fujita, S., T. Watanabe, and C. Kitajima
1980 Nutritional quality of *Artemia* from different localities as a living feed for marine fish from the viewpoint of essential fatty acids. *In* Persoone, L.G., P. Sorgeloos, D. Roels, and E. Jaspers (eds.), The brine shrimp *Artemia*, vol. 3, p. 277–290. Universal Press, Wettsen, Belgium.

Good, L.K., R.C. Bayer, M.L. Gallagher, and J.H. Rittenberg
1982 Amphipods as a potential diet for juveniles of the American lobster *Homarus americanus* (Milne Edwards). J. Shellfish Res. 2:183–187.

Govind, C.K.
1984 Development of asymmetry in the neuromuscular system of lobster claws. Biol. Bull. (Woods Hole) 167:94–119.

Govind, C.K., and J. Pearce
1986 Differential reflex activity determines claw and closer muscle asymmetry in developing lobsters. Science (Wash. DC) 233:354–356.

Hardy, A.
1970 The open sea: Its natural history. Part I: The world of plankton. Houghton Mifflin, Boston, 335 p.

Hedgecock, D., and K. Nelson
1978 Components of growth rate variation among laboratory cultured lobsters (*Homarus*), p. 125–137. *In* Proc. Annu. Meet. World Maricult. Soc. 9.

Herrick, F.H.
1895 The American lobster: A study of its habits and development. Bull. U.S. Fish. Comm. 15:1–252.
1911 Natural history of the American lobster. Bull. U.S. Fish. Comm. 29:147–408, 20 pls.

Hudon, C.
1987 Ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Îles de la Madeleine (Quebec). Can J. Fish. Aquat. Sci. 44:1855–1869.

Lang, F., C.K. Govind, W.J. Costello, and S.I. Greene
1977 Developmental neuroethology: Changes in escape and defensive behavior during growth of the lobster. Science (Wash. DC) 197:682–685.

Lavalli, K.L., and D.E. Barshaw
1989 Post-larval American lobsters (*Homarus americanus*) living in burrows may be suspension feeding. Mar. Behav. Physiol. 15:255–264.

Lebour, M.V.
1922 The food of plankton organisms. J. Mar. Biol. Assoc. U.K. 12:644–677.

McConaugha, J.
1985 Nutrition and larval growth. *In* Wenner, A.M. (ed.), Crustacean issues, vol. 2, p. 127–154. A.A. Balkema, Rotterdam & Boston.

Orth, R.J.
1973 Benthic infauna of eelgrass, *Zostera marina*, beds. Chesapeake Sci. 14:258–269.

Ortner, P.B., S.R. Cummings, R.P. Artring, and H.E. Edgerton
1979 Silhouette photography of oceanic zooplankton. Nature (Lond.) 277:50–51.

Reise, K.
1977 Predation pressure and community structure of an intertidal soft-bottom fauna. *In* Keegan, B.F., P.O. Ceidigh, and P.J.S. Boaden (eds.), Biology of benthic organisms: 11th European symposium on marine biology, Galway, October 1976, p. 513–519. Pergamon Press, NY.

Templeman, W.
1948 Growth per molt in the American lobster. Bull. Newfoundland Govt. Lab. 18:12-25. Avail. Dep. Fish. Oceans, St. John's, Newfoundland, Canada.

Templeman, W., and S.N. Tibbo
1945 Lobster investigations in Newfoundland 1938 to 1941. Dep. Nat. Resour. St. John's Research Bull. 16, Dep. Fish. Oceans, St. John's, Newfoundland, Canada, 98 p.

Wahle, R.A.
1990 Recruitment, habitat selection, and the impact of predators on the early benthic phases of the American lobster (*Homarus americanus* Milne Edwards). Ph.D. diss., Univ. Maine, Orono, 136 p.

Wieser, W.
1960 Benthic studies in Buzzards Bay. II. The meiofauna. Limnol. Oceanogr. 5:121–137.

Wilder, D.G.
1953 The growth rate of the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 10:371–412.

Williams, L.W.
1907 The stomach of the lobster and the food of larval lobsters. Annu. Rep. R.I. Comm. Inland Fish. 37:153–180 [avail. NMFS Woods Hole Lab., Woods Hole, MA 02543].

Diel Sampling of Migratory Juvenile Salmonids in the Columbia River Estuary

Richard D. Ledgerwood
Coastal Zone and Estuarine Studies Division
Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East, Seattle, Washington 98112-2097

Frank P. Thrower
Auke Bay Laboratory, Alaska Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 210155, Auke Bay, Alaska 99821

Earl M. Dawley
Coastal Zone and Estuarine Studies Division
Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA
2725 Montlake Boulevard East, Seattle, Washington 98112-2097

Abstract. – Beach and purse seine catches at Jones Beach, River kilometer 75, were used to examine diel movement patterns of juvenile chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss* as they migrated downstream in the Columbia River estuary. The patterns were monitored during five 24-hour periods in 1978, 1979, and 1980, and compared with patterns obtained from extensive morning-hour sampling conducted during 1979–83. Diel catch patterns were generally consistent among the sampling periods and there was reasonable agreement with morning-hour sampling. However, diel movement was different than that reported for salmonids in other river systems and in other locations in the Columbia River. The times and lateral position of greatest downstream movement which provided the largest catches of salmonid juveniles were as follows: sunrise to early afternoon nearshore for subyearling chinook salmon, sunrise to early afternoon midriver for yearling chinook salmon, midmorning to early evening nearshore and sunrise to early afternoon midriver for coho salmon, and noon to early evening midriver for steelhead. Decreased movement during darkness was apparent for all salmonids. No relationship between tidal cycle and catch was evident from either beach or purse seine sampling.

Manuscript accepted 24 July 1990.
Fishery Bulletin, U.S. 89:69–78 (1991).

Successful and cost-effective timing and survival studies for juvenile salmon and steelhead are dependent on understanding migratory behavior as well as sampling effectiveness. Literature regarding the migratory behavior of juvenile Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* indicates a wide variation in diel movement patterns, from greatest movement during daylight hours (Sims et al. 1976) to greatest movement at night (Smith et al. 1968) (see also Table 1). Catches used for the reported observations were obtained using an assortment of sampling equipment in large and small rivers and reservoirs during a range of turbidity conditions. Juveniles captured varied in life stage from emergent fry to migrating smolt. It was difficult to determine from some of the literature whether the greatest catches represented increased fish movement or times of greatest susceptibility to sampling equipment.

Personnel of the National Marine Fisheries Service conducted a sampling program at Jones Beach, Columbia River, kilometer (Rkm) 75, to examine diel movement patterns of juvenile chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, and steelhead in the upper Columbia River estuary. The objective was to establish the optimum time of day and lateral location for the most effective sampling of these fish during the peak of the spring migration. Also, this program was to provide data to compare with previous sampling results at Jones Beach which indicated midriver orientation of yearling fish, shore orientation of subyearling fish, and substantially decreased movement of shore-oriented migrants at night (Dawley et al. 1986).

Methods

Diel migration patterns were monitored using beach and/or purse seines during five 24-hour periods: 18–19 May 1978, 14–15 June 1978, and 14–15 May 1980 for beach seine; and 10–11 May 1979, 23–24 May 1979, and 14–15 May 1980 for purse seine. Sampling dates were based on peaks of juvenile salmonid migrations recorded in other years (1966–83) at Jones Beach (Dawley et al. 1986).

Purse seining was conducted midriver from the north edge of the ship channel toward Puget Island; beach

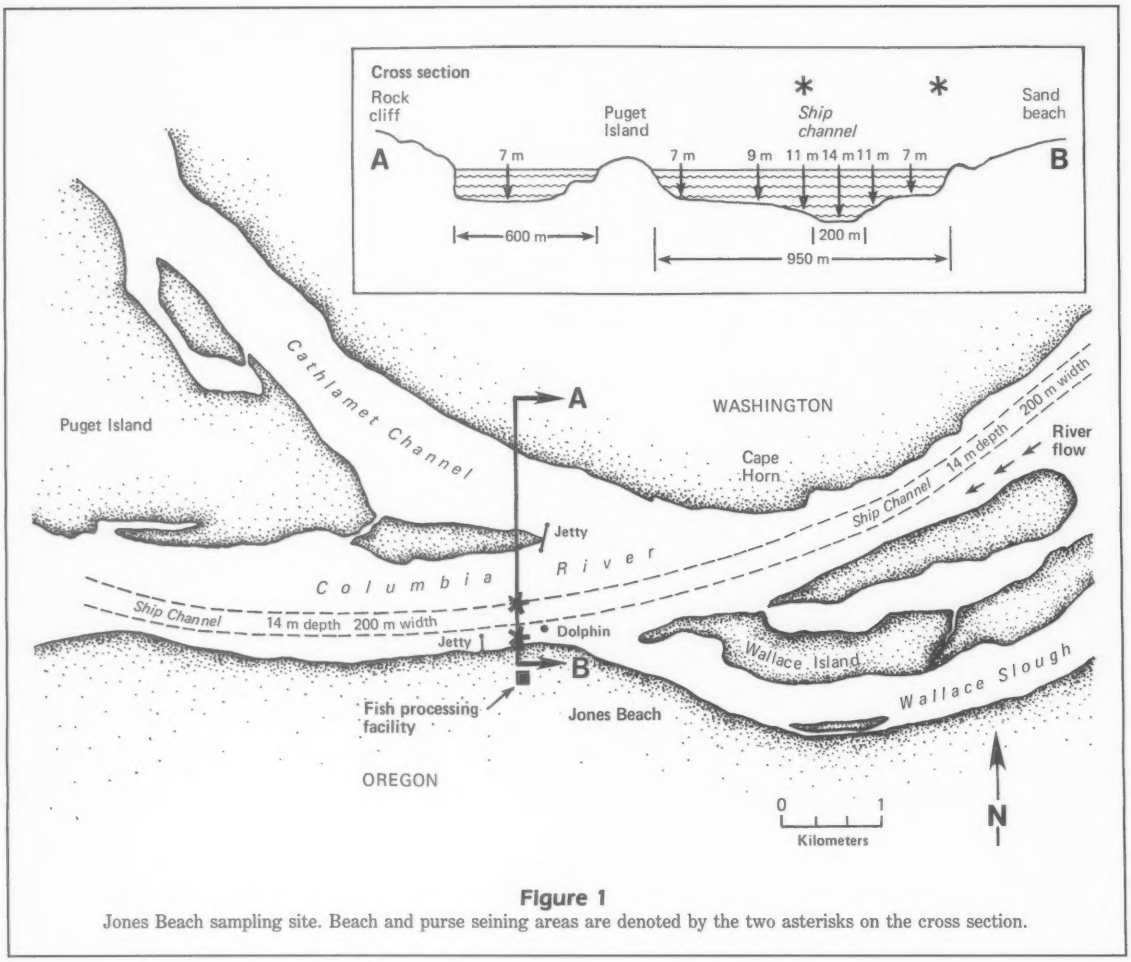


Figure 1
Jones Beach sampling site. Beach and purse seining areas are denoted by the two asterisks on the cross section.

seining was on the south shoreline, lateral to the purse seine site (Fig. 1).

Conditions of the Columbia River were different during each sampling period. River flows ranged from 6800 to 7600 m^3/second (U.S. Army Corps of Engineers 1978–80). Turbidity and water temperatures ranged from 5 to 11 Jackson Turbidity Units and 12° to 17°C, respectively. Tides at Jones Beach are semidiurnal (~7 hours of ebb and 4.5 hours of flood current); flow reversal occurs during flood tides throughout most of the year. River flows in the range of 5000–12,000 m^3/second generally occur during the period May through mid-July, and flood tide effects are diminished at these high flows.

Captured salmonids were anesthetized, identified to species, and enumerated (Dawley et al. 1985). Subyearling and yearling chinook salmon were separated on the basis of fork length; separation points were determined from the bimodal curves of length frequency. Verification of age from marked fish of known age (4.8–6.5% of catch) showed about 4% error in separation. All captured fish were either held in tanks onshore until sampling was complete and then released or transported downstream from the sampling area and released.

Beach seining

The beach seine was 95 m long by 5 m deep with 1–2 cm (stretch) webbing (Sims and Johnsen 1974). The net was fished downstream regardless of tidal influence. An anchor was used to secure one end of the net onshore and the opposite end, containing the bunt, was towed upstream at the 1-m depth contour, then arched

downstream and back to shore. The effective fishing depth of the net was 2–3 m in water up to 6 m deep. The net was pulled onto the beach which crowded the fish into the bunt for capture. Completion of each set required about 25 minutes; sets were made at 45-minute intervals.

Catch data from the first two or three seine sets on the first morning of each sampling period were not used for analysis of diel movement because some salmonids probably resided in the sampling area overnight, and the initial sets were used to clear the sampling site of those residents. Of the beach seine sets in each 24-hour period, 34% (11 of 32) were made during darkness and 66% (21 of 32) during daylight.

Purse seining

The purse seine was 206 m long by 11 m deep with 1–2 cm (stretch) webbing (Durkin and Park 1967). A depressor weight was used during the pursing operation to increase the effective fishing depth to about 6 m. The vessels used were a 10-m pontoon barge powered by outboard engines and an outboard- motored seine skiff; lights were mounted on the barge for night operation. A depth finder, a compass, and channel markers were used to locate the sampling site.

The seine was set near midriver in water 9–14 m deep, and towed upstream at constant power in a "U" configuration (Dawley et al. 1985). After 5 minutes, the ends of the net were brought together and the net bottom was closed (pursed) and hauled aboard the barge with a boom and hydraulic capstan. Then the cork line and webbing were retrieved and the catch was placed in 75-L containers supplied with circulating river water. Completion of each set required about 40 minutes; sets were made at 90-minute intervals. About 31% (5 of 16) of the purse seine sets were made during darkness and 69% (11 of 16) during daylight.

Data analysis

Each set represented one time interval within the 24-hour sampling period. Twice as many beach seine sets were made in each 24-hour period as purse seine sets; consequently, time intervals are one-half those for the purse seine. The catch per set (CPS) interval was calculated in terms of the percentage of the total 24-hour catch by species and stock. An overall percent CPS was calculated for each seine type by averaging interval values from the three appropriate sampling dates.

Diel catch data for each species were compared graphically and with linear regression to corresponding tidal heights at Jones Beach.

Results

During 14–15 May 1980, the only period we sampled with both beach and purse seines, the beach seine accounted for 79% of the total catch of subyearling chinook salmon (predominately fall race) (Van Hyning 1973), while the purse seine produced the largest catches of yearling fish: 92% of the yearling chinook salmon (predominately spring race); 82% of the coho salmon; 100% of the sockeye salmon *O. nerka*; and 97% of the steelhead. Daylight sampling in previous years produced similar beach seine to purse seine catch ratios (Dawley et al. 1986).

Examination of catch data indicated there was no apparent relationship to tidal variations for any species during any sampling period; correlation coefficients ranged from −0.51 to 0.14. Catch/tidal data are available upon request. Dawley et al. (1986) also observed a lack of correlation between tidal cycles and beach seine catches of subyearling chinook salmon from the Columbia River estuary.

Subyearling chinook salmon

Beach seine catches of subyearling chinook salmon (13,513 fish) peaked during the interval about 1.5 hours after sunrise (6.9% CPS) followed by steady catches during the daylight intervals, each near 4.0% CPS. About 1.5 hours before sunset, a second, smaller peak was observed in two intervals (CPS of 5.2% each), followed by a sharp and continued decrease with darkness through the night intervals (average CPS = 0.9%). The night catch was 10.2% (3.8 SD) of the total catch for a 24-hour period. Catches increased again about 45 minutes before sunrise (Fig. 2A).

Purse seine catches of subyearling chinook salmon (1461 fish) increased just before sunrise and decreased throughout the day (Fig. 2B). Again, only 10% (1.7 SD) of the total purse seine catch was at night.

Coho salmon

About 21% of the yearling coho salmon captured were from beach seining (1092 by beach seine and 3990 by purse seine). The June 1978 sampling period produced only 17 fish and was not included in the assessment of movement behavior. Beach seine catches in daylight were low until about 1000 hours then generally increased, with large fluctuations between intervals, to a peak at about 1430 hours (10.7% CPS) (Fig. 2C). In the late afternoon and evening, catches generally decreased with large fluctuations between intervals. The CPS dropped at dusk to 2.5% followed by lower catches during darkness. The night catch averaged

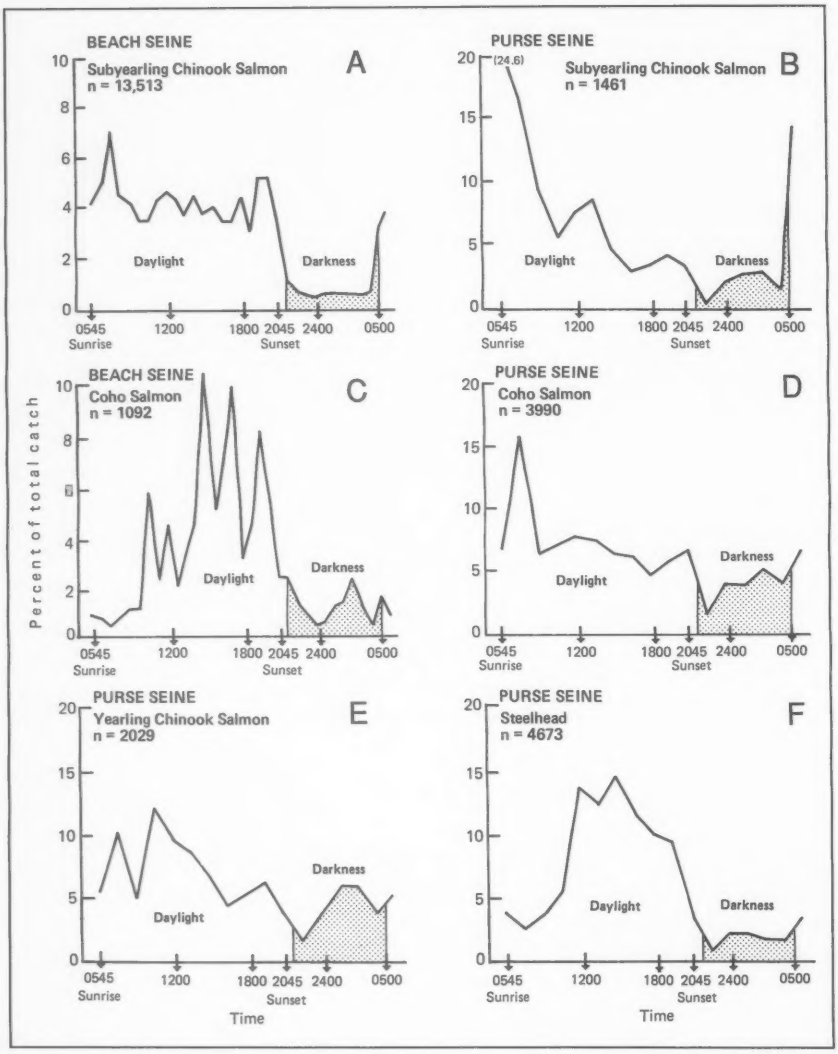


Figure 2
Diel catch patterns for chinook salmon, coho salmon, and steelhead from beach and purse seine sampling at Jones Beach, 1978–80 (samples combined and averaged).

13.7% of the total catch for the two 24-hour sampling periods.

Purse seine catches peaked during the interval about 1.5 hours after daylight (15.8% CPS) and remained near 6.5% CPS throughout the daylight intervals the (Fig. 2D). Catches decreased in the night intervals to an average 3.7% CPS; 18.5% (4.6 SD) of the CPS was obtained during darkness.

Yearling chinook salmon

The majority of yearling chinook salmon migrated mid-river; purse seine catches totaled 2029 fish compared with 113 from the beach seine. The peak catch with the purse seine was during the interval 0946 to 1115 hours (12.3% CPS). Overall, 46% of the total catch was taken in 31% of the sets (1.5 hours after sunrise to about 1330 hours) (Fig. 2E). Purse seine catches were smallest from dusk to midnight (average 3.2% CPS), with larger catches occurring during the remainder of the night intervals (average 5.4% CPS). The night catch was 21.1% (7.0 SD) of the total purse seine catch for a 24-hour period.

Sockeye salmon

Sockeye salmon juveniles were caught only in the purse seine (222 fish), with 15% (6.3 SD) captured at

night. An insufficient number of fish were captured to allow a more detailed analysis of the diel migration pattern.

Steelhead

Over 98% of the juvenile steelhead were caught by purse seine (4673 by purse seine and 74 by beach seine). Purse seine catches were moderate in the four intervals after sunrise (average 4% CPS), peaked at the interval from 1416 to 1545 hours (14.6% CPS), decreased at dusk, and remained low throughout the night intervals (average 1.7% CPS) (Fig. 2F). The night catch was 8.7% (1.0 SD) of the total catch for a 24-hour period.

Discussion

Catch data from our beach and purse seines appear to represent movement and position of juvenile salmonids during their migration through the upper Columbia River estuary. Catches of subyearling chinook salmon at both purse and beach seining sites indicate a substantially decreased migration during darkness. Beach (nearshore) and purse (midriver) seine catches of coho salmon indicate a fairly uniform migration throughout the daylight period. Data obtained for yearling chinook salmon, sockeye salmon, and steelhead indicate a midriver orientation with decreased migration during darkness. Other researchers have reported different diel movement patterns, but conditions, equipment, and life stages of the fish sampled are so variable that direct comparison between experiments is difficult (Table 1).

Table 1

Summary of diel observations of juvenile chinook and coho salmon and steelhead in various Pacific Northwest and Alaska river systems.

Environment	Life stage	Location	Method	Pertinent observations of movement behavior	Source
Yearling chinook salmon					
River	Smolt	Central Ferry Bridge (Snake R.)	Fyke net	Largest catches between 0300 and 0600 h, smallest catches between 0600 and 1200 h. Largest catches from shoreline areas during low and medium river flow, and midriver areas during high flow. Catches uniform in number from surface to bottom.	Mains and Smith 1964
River	Smolt	Byer's Landing (mid-Columbia R.)	Fyke net	Largest catches (70%) between 1800 and 0600 h. Largest catches in shoreline areas. Largest catches in surface water (0.8 m).	Mains and Smith 1964
Reservoir	Smolt	John Day (Columbia R.)	Purse seine	Largest catches during daylight (0700–2100 h).	Sims et al. 1976
Reservoir	Smolt	Lower Monumental (Snake R.)	Monofilament gillnet	Largest catches at night; 92% of total catch. Catches in the upper 7.3 m were 5 during the day and 109 at night, and catches below 7.3 m increased from 6 during the day to 19 at night. Largest catches in central portion of reservoir, day and night.	Smith 1974
Reservoir	Smolt and fry	Mayfield (Cowlitz R.)	Floating fish trap	Largest catches (82% of total obtained between 2000 and 0800 h.	Allen 1965
Reservoir	Fingerling and fry	Upper Mayfield (Cowlitz R.)	Trawl and gillnet	Largest catches during darkness or periods of high turbidity (trawl). Largest catches (87%) in upper 7.3 m. Movement of fish not strongly downstream.	Smith et al. 1968
Reservoir	Smolt and fingerling	North Fork (Clackamas R.)	Gillnet	Largest catches during darkness near surface (0–5 m) over deep water (15 m).	Korn et al. 1967
Reservoir	Smolt	Rocky Reach (Columbia R.)	Sonar	Highest movement between dusk and dawn.	Leman 1978

Table 1 (continued)

Environment	Life stage	Location	Method	Pertinent observations of movement behavior	Source
Yearling chinook salmon (continued)					
Dam	Smolt	John Day (Columbia R.)	Dip net and airlift pump	Largest catches (92% of total) between dusk and dawn (8.5-h period). Turbine intake, 20 m below surface.	Sims et al. 1976 Sims and Ossiander 1981
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in turbine intake	Largest catches (94%) at night (1900–0700 h). Largest catches (75% of total) from upper third of intakes (top of turbine intake, 6 m below surface).	Long 1968
			Dip net in gatewell	Largest catches during daylight (0700–2100 h) with only 11% of total caught in darkness (8.5-h period).	Sims et al. 1976 Nichols 1979
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in sluiceway	Largest catches in daylight (0800–1400 h) with few fish after dark; 3-ft deep surface flow over sluiceway gate. Largest catches near dusk (1700–2200 h) with few fish at other periods; 2-ft deep surface flow over sluiceway gate.	Nichols 1979
Subyearling chinook salmon					
Estuary	Smolt	Puget Island and Jones Beach (Columbia R. estuary)	Beach seine	90% of catch from daylight sets (0600–2100 h). Largest catches during early morning and at dusk.	Dawley et al. 1986
River	Fingerling and fry	Sixes R. (Oregon R.)	Traps	Both emergence of fry from the gravel and downstream migration of fry and fingerling primarily during darkness.	Reimers 1973
Reservoir	Smolt	John Day (Columbia R.)	Purse seine	Largest catches during daylight (0700–2100 h).	Sims et al. 1976
Dam	Smolt	John Day (Columbia R.)	Dip net and airlift pump in gatewell	Largest catches (88% of total) between dusk and dawn. Turbine intake, 20 m below surface.	Sims et al. 1976 Sims and Ossiander 1981
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in turbine intake	Largest catches (67%) at night (1900–0700 h). Largest catches (49% of total) from upper third of water column (4.4 m) entering the intakes (top of turbine intake, 6 m below surface).	Long 1968
			Dip net in gatewell	Largest catches during daylight (0700–2100 h) with 10% of total caught in darkness (8.5-h period). Turbine intake, 6 m below surface.	Sims et al. 1976 Nichols and Ransom 1980
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in sluiceway	Largest catches in daylight (0600–0700 and 1400–2100 h) with few fish after dark; 3-ft deep surface flow over sluiceway gate.	Nichols and Ransom 1980
Coho salmon					
Estuary	Smolt	Columbia R.	Purse seine	Largest catches at midday (1000–1400 h).	Durkin 1982
River	Smolt	Minter Creek (Puget Sound)	Trap	Largest catches at dawn and dusk.	Salo and Bayliff 1958
River	Smolt	Taku R. (S.E. Alaska)	Scoop trap	Largest catches at dawn and dusk.	Meehan and Siniff 1962
Reservoir	Smolt	Brownlee (Snake R.)	Fyke net	Largest catches at dawn and dusk.	Monan et al. 1969
Reservoir	Smolt	John Day (Columbia R.)	Purse seine	Largest catches during daylight (0700–2100 h).	Sims et al. 1976

Table 1 (continued)

Environment	Life stage	Location	Method	Pertinent observations of movement behavior	Source
Coho salmon (continued)					
Reservoir	Smolt and fingerling	North Fork (Clackamas R.)	Gillnet	Largest catches at dawn and dusk; near surface during darkness and deeper during daylight.	Korn et al. 1967
Reservoir	Smolt and fingerling	Round Butte (Deschutes R.)	Gillnet	Few fish captured during daylight during any season. During spring migration period, smolts captured principally near surface (0–3.7 m).	Korn et al. 1967
Reservoir	Fingerling and fry	Upper Mayfield (Cowlitz R.)	Trawl and gillnet	Largest catches during darkness or periods of high turbidity (trawl). Largest catches (87%) near surface (0–7.3 m). Movement of fish not strongly downstream.	Smith et al. 1968
Dam	Smolt	John Day (Columbia R.)	Dip net in gatewell of dam	Largest catches during darkness (2100–0700 h). Turbine intake, 20 m below surface.	Sims et al. 1976
Dam	Smolt	The Dalles (Columbia R.)	Dip net in gatewell of dam	Largest catches during daylight (0700–2100 h). Turbine intake, 6 m below surface	Sims et al. 1976
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in sluiceway	Largest catches in daylight (0800–1400 h) with few fish after dark; 3-ft deep surface flow over sluiceway gate. Largest catches near dusk (1700–2200 h) with few fish at other periods; 2-ft deep surface flow over sluiceway gate.	Nichols 1979
Steelhead					
Reservoir	Smolt	John Day (Columbia R.)	Purse seine	Largest catches during daylight (0700–2100 h).	Sims et al. 1976
Reservoir	Smolt	Lower Monumental (Snake R.)	Monofilament gillnet	Largest catches at night; 76% of daily total. Catches in the upper 7.3 m increased from 146 during the day to 396 at night and catches below 7.3 m from 56 during the day to 420 at night. Uniform distribution across the reservoir day and night.	Smith 1974
Reservoir	Smolt and fry	Mayfield (Cowlitz R.)	Floating fish trap	Largest catches (82% of total) obtained between 2000 and 0800 h.	Allen 1965
Reservoir	Fingerling and fry	Upper Mayfield (Cowlitz R.)	Trawl and gillnet	Largest catches during darkness or periods of high turbidity (trawl). Largest catches (87%) in upper 7.3 m. Movement of fish not strongly downstream.	Smith et al. 1968
Reservoir	Smolt and fingerling	North Fork (Clackamas R.)	Gillnet	Largest catches (few fish) during darkness near surface over deep water.	Korn et al. 1967
Dam	Smolt	John Day (Columbia R.)	Dip net and airlift pump in gatewell of dam	Largest catches (77% of total) between dusk and dawn (8.5 h period). Turbine intake, 20 m below surface.	Sims et al. 1976
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in turbine intake	Largest catches (85%) at night (1900–0700 h). Largest catches (72% of total) from the upper third of the water column (4.4 m) entering the intakes (top of turbine intake, 6 m below surface).	Long 1968

Table 1 (continued)

Environment	Life stage	Location	Method	Pertinent observations of movement behavior	Source
Steelhead (continued)					
Dam	Smolt	The Dalles (Columbia R.)	Fyke net in turbine intake	Largest catches during daylight with only 29% of total caught in darkness (8.5 h period). Turbine intake, 6 m below surface.	Sims et al. 1976
Dam	Smolt	The Dalles (Columbian R.)	Fyke net in sluiceway	Largest catches in daylight (0800–1400 h) with few fish after dark; 3-ft deep surface flow over sluiceway gate. Largest catches near dusk (1700–2200 h) with few fish at other periods; 2-ft deep surface flow over sluiceway gate.	Nichols 1979

Variability of catch between sets and sampling periods was higher for yearling chinook salmon than for other salmonids. The origin of marked fish varied substantially among the three purse-seine sampling periods (Table 2). The largest portions of the catch originated in the Willamette, mid-Columbia, and Snake Rivers for the first, second, and third sampling periods, respectively. Stock differences and changes in abundance among stocks during the diel sampling periods may have caused the higher variability in the catch.

We found reasonable agreement among the diel catch patterns reported here and those from extensive morning sampling (2615 sets) at Jones Beach in May and June 1979–83 (Dawley et al. 1986) (Fig. 3). A noteworthy exception was that beach seine catches near sunrise were lower during the diel study because sets were made before sunrise to remove fish which resided in the area overnight.

It is generally agreed that net avoidance is probably greatest in daylight; therefore, decreased net catches at night should represent decreased fish abundance in the water sampled. It seems unlikely that decreased catches at Jones Beach during darkness were caused by surface- or midwater-oriented juveniles maintaining their position against current velocities up to 5 km/hour. Data obtained at Jones Beach by Dawley et al. (1986) showed that marked subyearling chinook salmon released into the shoreline sampling area at night were recaptured at a much higher rate than marked fish released during daylight (30.6 vs. 8.0%). Because midriver-oriented yearling fish do not appear in shoreline areas at Jones Beach during darkness, they probably hold near the bottom,

Table 2

Origin of marked yearling chinook salmon captured by purse seine during diel sampling, 1979 and 1980.

	Sampling dates		
Origin	10–11 May 1979	23–24 May 1979	14–15 May 1980
	% of marks		
Snake River	7	19	60
mid-Columbia River	13	47	40
Transported and released downstream from Bonneville Dam	33	28	0
Willamette River	40	0	0
Lower Columbia River	7	6	0

Table 3

Measured movement rates of juvenile salmonids and water velocities in a 155-km reach of the Columbia River between Bonneville Dam and Jones Beach at two volumes of river flow.

River flows (1000 m^3/s)	Water velocity (km/h)[b]	Movement rates (km/h)[a]			
		Chinook salmon		Coho salmon	Steelhead
		Subyearling	Yearling		
8.1 ± 0.5	4.8	0.9	0.8	1.4	3.2
11.3 ± 0.5	5.0	1.0	—	0.9	1.7

[a] Zero to nine marked groups were available for each calculation of average movement rate at these designated river flows (Dawley et al. 1986).
[b] From Blahm (1974).

particularly in deep areas of low current velocity. This premise is supported by studies on water velocity (Blahm 1974) and the movement rates of marked juvenile salmon released below Bonneville Dam and recovered at Jones Beach (Dawley et al. 1986) (Table 3). In all cases, fish migration speeds from release site to capture in the estuary were less than water velocity (Dawley et al. 1986).

In conclusion, the most appropriate times and locations for sampling to attain maximum CPSs are as follows: Subyearling chinook salmon, sunrise to early afternoon nearshore; yearling chinook salmon, sunrise to early afternoon midriver; yearling coho salmon, midmorning to early evening nearshore and sunrise to early afternoon midriver; juvenile steelhead, noon to early evening midriver.

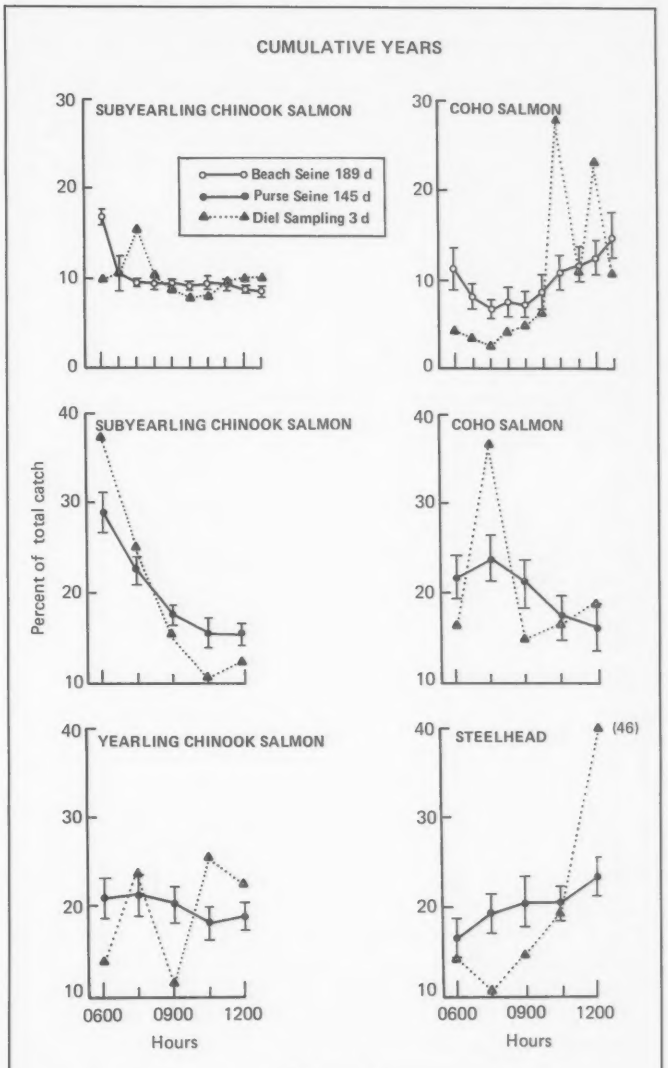


Figure 3

Percent total catch of juvenile salmonids during morning hour sampling at Jones Beach, Columbia River (1979–83) compared with diel sampling results (mean value per time interval and 95% confidence limits); d = total number of sampling days used for each estimate.

Acknowledgment

The authors acknowledge Dr. Theodore Blahm (deceased) for providing inspiration and encouragement while conducting this study.

Citations

Allen, R.
1965 Juvenile fish collector operation at Lake Mayfield July 1, 1964 to June 30, 1965. Report to Bureau of Commercial Fisheries, Contract 14-17-0001-1357. Wash. Dep. Fish., Olympia, 23 p.

Blahm, T.H.
1974 Gas supersaturation research, Prescott Facility–1974. Report to U.S. Army Corps of Engineers, Contract DACW57-74-F-0414. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98112, 34 p.

Dawley, E.M., R.D. Ledgerwood, and A.L. Jensen
1985 Beach and purse seine sampling of juvenile salmonids in the Columbia River estuary and ocean plume, 1977–1983; Vol. I. Procedures, sampling effort, and catch data. NOAA Tech. Memo. NMFS F/NWC-74, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98112, 260 p.

Dawley, E.M., R.D. Ledgerwood, T.H. Blahm, C.W. Sims, J.T. Durkin, R.A. Kirn, A.E. Rankis, G.E. Monan, and F.J. Ossiander
1986 Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966–1983. Report to Bonneville Power Administration, Portland, Oregon. Contract DE-A179-848BP39652. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98112, 256 p.

Durkin, J.T.
1982 Migration characteristics of coho salmon (*Oncorhynchus kisutch*) smolts in the Columbia River and its estuary. *In* Kennedy, V. (ed.), Estuarine comparisons, p. 365–375. Academic Press, NY.

Durkin, J.T., and D. L. Park
1967 Purse seine for sampling juvenile salmon. Prog. Fish-Cult. 29:56–59.

Korn, L.M., L.H. Hreha, R.G. Montagne, W.G. Mullarkey, and E.J. Wagner
1967 The effects of small impoundments on the behavior of juvenile anadromous salmonids. Final Report to U.S. Bureau of Commercial Fisheries, Contract 14-17-0001-597,767,917, 1093, and 1238. Fish Comm. Oreg., Res. Div., Clackamas, 127 p.

Leman, B.D.
1978 Coordinated spilling at Columbia River dams during low river flows; response by Public Utility Districts. Unpubl. manuscr., Chelan County, Public Utility District #1, Wenatchee, WA, 15 p.

Long, C.
1968 Diel movement and vertical distribution of juvenile anadromous fish in turbine intakes. Fish. Bull., U.S. 66: 599–609.

Mains, E.M., and J. M. Smith
1964 The distribution, size, time and current preferences of seaward migrant chinook salmon in the Columbia and Snake Rivers. Wash. Dep. Fish., Fish. Res. Pap. 2(3):5–43.

Meehan, W.R., and D.B. Siniff
1962 A study of the downstream migrations of anadromous fish in the Taku River, Alaska. Trans. Am. Fish. Soc. 91: 399–407.

Monan, G.E., R.J. McConnell, J.R. Pugh, and J.R. Smith
1969 Distribution of debris and downstream-migrating salmon in the Snake River above Brownlee Reservoir. Trans. Am. Fish. Soc. 98:239–244.

Nichols, D.W.
1979 Passage efficiency and mortality studies of downstream migrant salmonids using The Dalles ice-trash sluiceway during 1978. Report to U.S. Army Corps of Engineers, Contract DACW 57-78-C-0058. Oreg. Dep. Fish Wildl., Portland, 28 p.

Nichols, D.W., and B.H. Ransom
1980 Development of The Dalles Dam ice and trash sluiceway as a downstream migrant bypass system, 1980. Final report to U.S. Army Corps of Engineers, Contract DACW 57-78-C-0058. Oreg. Dep. Fish Wildl., Portland, 37 p.

Reimers, P.E.
1973 The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Res. Rep. Fish Comm. Oreg. 4(2): 3–43.

Salo, E.O., and W.H. Bayliff
1958 Artificial and natural production of silver salmon, *Oncorhynchus kisutch*, at Minter Creek, Washington. Wash. Dep. Fish. Res. Bull. 4:1–76.

Sims, C.W., and R.C. Johnsen
1974 Variable mesh beach seine for sampling juvenile salmon in the Columbia River estuary. Mar. Fish. Rev. 36(2):23–26.

Sims, C.W., and F.J. Ossiander
1981 Migrations of juvenile chinook salmon and steelhead trout in the Snake River from 1973 to 1979, a research summary. Final report to U.S. Army Corps of Engineers, Contract DACW68-78-C-0038. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98112, 53 p.

Sims, C.W., R.C. Johnsen, and W.W. Bentley
1976 Effects of power peaking operations on juvenile salmon and steelhead trout migrations, 1975. Final report to U.S. Army Corps of Engineers, Contract DACW68-77-C-0025. Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98112, 61 p.

Smith, J.R.
1974 Distribution of seaward migrating chinook salmon and steelhead trout in the Snake River above Lower Monumental Dam. Mar. Fish. Rev. 36(8):42–45.

Smith, J.R., J.J. Pugh, and G.E. Monan.
1968 Horizontal and vertical distribution of juvenile salmonids in upper Mayfield Reservoir, Washington. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 566, 11 p.

U.S. Army Corps of Engineers
1978–1980 Annual fish passage reports, Columbia and Snake Rivers, for salmon, steelhead, and shad. U.S. Army Corps of Engineers, North Pac. Div., Portland, OR, 41 p.

Van Hyning, J.M.
1973 Factors affecting the abundance of fall chinook salmon in the Columbia River. Res. Rep. Fish Comm. Oreg. 4(1):3–87.

Fishery Characteristics, Growth, and Movements of the Spiny Lobster *Panulirus argus* in Bahia de la Ascension, Mexico

Enrique Lozano-Alvarez
Patricia Briones-Fourzan
Universidad Nacional Autonoma de Mexico
Instituto de Ciencias del Mar y Limnologia, Estacion "Puerto Morelos"
P.O. Box 1152, Cancun, Q.R., 77500 Mexico

Bruce F. Phillips
Commonwealth Scientific and Industrial Research Organization (CSIRO)
Marine Laboratory, P.O. Box 20, North Beach, W.A., 6020 Australia

Abstract.—In Bahía de la Ascensión, México, the fishery for *Panulirus argus* is based on artificial shelters called "casitas." Highest catch-per-unit-effort (kg tails/boat·day) in the fishery occurs each year immediately after the opening of the fishing season, and declines sharply over the next months. This trend probably reflects combined effects of natural mortality, fishing mortality, and emigration of lobsters from the bay.

In 1985, 3470 tagged lobsters were released during the closed season, and 849 (24.5%) were recaptured by fishermen, mainly during the first three months of the following fishing season. In 1986, an additional 1324 tagged lobsters were released, and 407 (30.7%) were subsequently recaptured. Growth of recaptured lobsters was highly variable, and sexes had different growth rates, that of males being higher. Von Bertalanffy parameters for each sex were calculated using two different techniques; most reasonable estimates were obtained by a maximum likelihood approach. Ninety-nine percent of the recaptured lobsters were caught within the bay, but movements generally tended to be toward the reef in front of the bay. Longest straight-line distance moved was 45 km.

The population fished in the bay was composed entirely of juveniles, and we hypothesize that an unfished population of adults exists outside the bay. Testing of this hypothesis would benefit future management plans. In addition, the long-term effects of casitas on the lobster population and on the ecology of the seagrasses and their associated benthic communities need to be understood.

Manuscript accepted 12 September 1990.
Fishery Bulletin, U.S. 89:79–89 (1991).

Panulirus argus accounts for approximately one-third of México's spiny lobster production of about 2400 t (mean for 1978–87), 80% of which is produced in the state of Quintana Roo (Secretaría de Pesca 1987). The fishery for lobsters in Bahía de la Ascensión began in 1965. Initially, traps and skin diving were used, but in 1968 "casitas cubanas" were introduced (Miller 1982). These "casitas" consist of a frame of about 1.8 × 1.2 m made of the trunks of a local palm, and a "roof" of the same wood, metal, asbestos or, more recently, ferrocement. Casitas are sunk over seagrass-covered bottom. The fishermen check the casitas by skin diving, and catch the lobsters with a gaff (Lozano et al. 1989). The bottom of the bay suitable for setting casitas has been divided into several parcels of different sizes, alloted to the older fishermen. Miller (1982) suggested that the casitas might increase the fishing pressure on the population and cause overfishing, and Eggleston et al. (1990) propose that casitas provide critical refuge for juvenile lobsters from their predators. The long-term effects of casitas on the lobster population remain to be determined.

Here we report the results of an investigation using tag and recapture methods to study the structure, movements, and growth rates of the spiny lobster population in Bahía de la Ascensión during 1985–87.

Methods

Fishing methods in Quintana Roo

The coast of Quintana Roo can be divided into three areas on the basis of the lobster fisheries (Fig. 1a):

In the northern area, from Holbox to Tulum and especially around Isla Mujeres, the fishery is well developed. Lobsters are caught mainly by traps in depths of 15–60 m, and by Scuba and "hookah" diving to depths near 40 m. An annual migration of lobsters occurs along the northeastern coast of the Yucatan Peninsula in a southerly direction, at the end of autumn or in winter (Kanciruk and Herrnkind 1978). During this migration, fishermen use lobster bottom-nets in areas 2–10 m deep. Twelve cooperatives, involving 65% of the 1084 lobster fishermen of the state, operate in the northern area.

In the central area, where Bahía de la Ascensión is located, skin diving and "casitas cubanas" are used. In this area, where three cooperatives

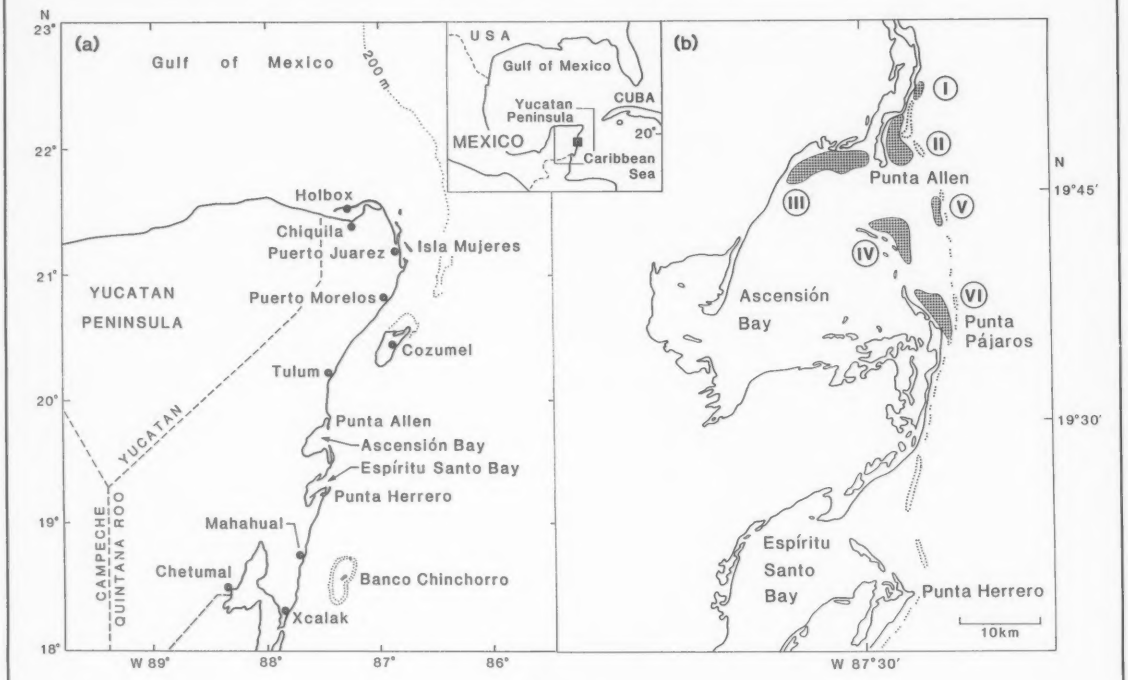


Figure 1

(a) The coast of Quintana Roo, showing the main fishing localities for *Panulirus argus*. (b) The six sampling zones for tagging operations in Bahía de la Ascensión.

with 21% of the fishermen operate, lobster fishing is limited to a depth of approximately 15 m.

In the southern zone, including Chinchorro Bank, three cooperatives involving 14% of the fishermen catch lobsters exclusively by skin diving with a gaff, to a depth of approximately 15 m (Secretaría de Pesca 1987).

Study site

Bahía de la Ascensión (Fig. 1b) is an open, shallow bay (<6 m) approximately 740 km^2 in area. Several coral banks follow an ancient shore line along the mouth of the bay (Jordán 1988) and form an interrupted reef. This reef reduces wave surge, and hence the bay has relatively calm waters.

The bay is bordered by mangrove and grass swamps and has several mangrove keys in its central and southern parts. The outer half of the bay is dominated by hard, sandy substrates with extended seagrass areas, whereas the inner half of the bay is shallow (<2 m), with mostly soft, unconsolidated sediments.

The fishery

Up to a maximum of 108 lobster fishermen in the area belong to a cooperative named "Pescadores de Vigía Chico," based at Punta Allen. A team that fishes the casitas in an owner's parcel during the fishing season consists of two or three fishermen (the parcel owner and one or two assistants). The number of casitas per parcel varies, and some owners claim to have more than 1000. The total number of casitas in the entire fishing ground of the cooperative was estimated at approximately 20,000, based on interviews of all fishermen in the cooperative. The fishermen catch lobsters mainly in the outer half of the bay, where seagrass is more abundant. There are no parcels in the inner half because the bottom is not suitable for casitas and the water is usually too turbid for diving. Regulations for this fishery include a closed season from 16 March to 15 July, a minimum size limit of 135 mm tail length (≈74 mm carapace length), and a prohibition on the catching of egg-bearing females. Only the tails are utilized. Tails are graded according to weight, packed in 10-pound (4.650 kg) boxes, and frozen.

Detailed data on monthly production (in boxes) of the cooperative during the 1985–86 fishing season were obtained from the processing plant. The relationship between tail weight (TW, in g) and carapace length (CL, in mm) was estimated by linear regression expressed as a power equation,

$$TW\ (g) = 0.00203\ CL\ (mm)^{2.5503}$$

where $N = 98$, $r^2 = 0.98$, CL range = 44.7–137.9 mm.

Data on catch in kg/tail weight of each fishing team were available since 1981 and converted to catch-per-unit-effort (CPUE, catch/boat·day). A Leslie analysis (Leslie and Davis 1939) was applied to the CPUE data to estimate the fishing mortality (F).

Tagging

Lobsters were tagged in Bahía de la Ascensión during 16 April–14 May 1985, and 18 May–30 June 1986, i.e., during the closed season. The area of the bay where casitas are distributed was divided into six sampling zones (Fig. 1b). Lobsters were tagged in all zones during 1985, and in zones II–VI in 1986. Chittleborough's (1974) western rock lobster tags were used. Only animals ⩾ 44 mm CL were tagged in order to reduce incidental mortality which might occur on smaller animals (Chittleborough 1974). Tags were inserted into the dorsolateral extensor muscle between the cephalothorax and first abdominal segment. After tagging, the lobsters were immediately released where they had been caught. Underwater observations revealed that after a few minutes, the tagged lobsters returned under the same casita.

Tag number, date, release location, sex, reproductive state, and CL (± 0.1 mm measured from between the rostral horns to the posterior dorsal edge of the carapace) were recorded. Fishermen were requested to keep the head of a recaptured lobster with its tag so the CL could be measured, and to provide the recapture date and location. The tagging program was advertised widely, and a reward was offered in the form of a lottery to encourage tag returns.

Analyses of growth data

The analysis of growth using capture-recapture data was performed using Fabens' method (1965), and a technique developed by M. Palmer (CSIRO Div. Math. Stat., Floreat Park, W.A. 6014, Australia). This technique assumes an individual lobster grows exponentially with time:

$$y = a\,(1 - e^{bt}) + E$$

where y = CL (mm), a = asymptotic CL (mm), b = a growth coefficient, t = time, and E = residuals. A mean value of 6 mm CL obtained from 50 settling pueruli was introduced as a starting size (zero age) into the model.

Parameters for the model, including variability of individual growth, were estimated using a multivariate Gaussian distribution. The residuals around an individual's curve (E) were assumed to be independent Gaussian normal with constant variance. The likelihood estimate, assuming that individual coefficients are known for an individual, was

$$L_i = p\,(y \mid a,b)\ p\,(a,b)$$

where L_i = initial length, and p(.|.) denotes a probability distribution.

Since the individual animal's coefficients were unknown, we consider them as "nuisance" parameters and integrate them out of the likelihood, giving

$$l_i = \int_{-\infty}^{\infty} p\,(y \mid a,b)\ p(a,b)\ da\,db$$

where l_i is the likelihood for the i^{th} individual. Then the product of the individual likelihood must be maximized to find the estimates of the population parameters. A convenient algorithm to use in this case is the EM algorithm (Dempster et al. 1977). Details of its application in this context are in Laird et al. (1987), Palmer (1986), and Palmer et al. (1988).

Although the time between subsequent captures was known, the age at first capture was unknown. A probability distribution for this unknown parameter was also assumed, but now the initial time is treated as "missing" and is removed from the likelihood by integrating it out. The likelihood for the i^{th} animal is now of the form

$$l_i = \int_{0}^{\infty} \int_{-\infty}^{\infty} p(y \mid a,b,t_1)\ p(a,b)\ da\,db\,dt_1.$$

Maximum likelihood is used to estimate both the growth parameters and the distribution of initial ages. The method of constructing and maximizing the likelihood is described in Palmer et al. (1988).

Mean weekly growth rates (Hunt and Lyons 1986) of recaptured lobsters were analysed to determine if there were significant changes in growth rate along their size range.

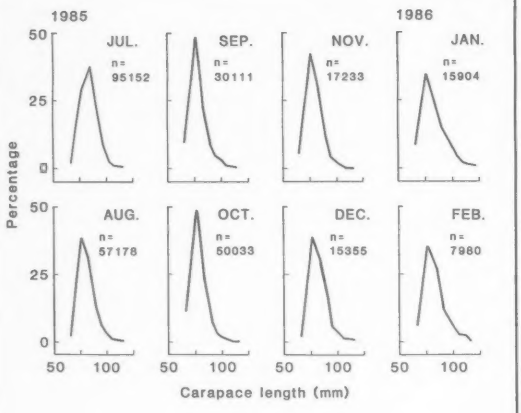


Figure 2
Monthly size-frequency distribution of the commercial catch (July 1985–February 1986) of *Panulirus argus* in Bahía de la Ascensión, obtained by converting tail weight (g) to carapace length (mm).

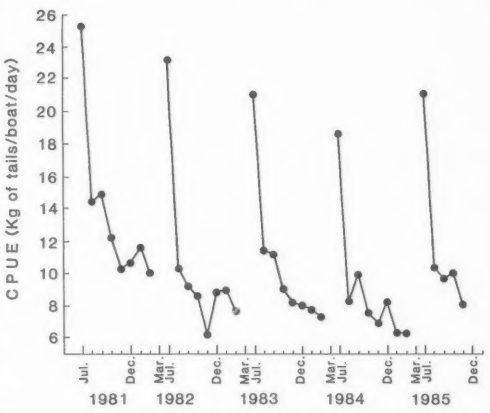


Figure 3
CPUE (kg tails/boat·day) of *Panulirus argus* for the fishing seasons 1981–82 to 1985–86 in Bahía de la Ascensión (no data available for January–March, 1986).

Results

Commercial catch and size composition

The total catch of lobster tails in Bahía de la Ascensión for 1985–86 was 42.5t, and for 1986–87, 63.0t. The size composition of the commercial catch for July 1985–February 1986 is shown in Figure 2. Data for March were insufficient and not included. There was a mode around the minimum legal size throughout the fishing season, except in July.

The CPUE (catch/boat·day) data trends were similar each year (Fig. 3). The highest CPUE occurred during 16 July–15 August, i.e., immediately after the opening of the fishing season, followed by a sharp decline over the next few months. This trend probably reflected both fishing and natural mortality, as well as emigration.

The values of F (fishing mortality), between 1.25 and 2.80, derived using a Leslie analysis (Leslie and Davis 1939) were highly influenced by the July data, which were the annual peaks (Fig. 3), implying a different F for that month. Therefore, the results of the analysis were biased and could not be considered a good estimate of mortality.

Tagging results

Of the total 3893 lobsters caught in 1985, 3470 were large enough to be tagged (Fig. 4a). The male:female ratio of the captured population was 1.14:1, and that of the tagged population was 1.13:1. Of the total 1403 lobsters caught during 1986, 1324 were tagged (Fig. 4b). The male:female ratios of both the captured and tagged populations were 1.04:1. The size range of both sexes was similar for both years.

A total of 849 tagged lobsters were recaptured during the 1985–86 fishing season (24.5% of total tagged in 1985). None of the animals tagged in 1985 were recaptured during the 1986 tagging period. However, four lobsters tagged in 1985 were recaptured during the 1986–87 fishing season. The male:female ratio of recaptured animals was 1.14:1. Lobsters were recaptured in all sampling zones in the bay, as well as at some localities outside of the bay.

A total of 407 lobsters were recaptured during the 1986-87 fishing season (30.7% of total tagged in 1986); the male:female ratio was 1.08:1. In this season, no lobsters were recaptured outside the cooperative's fishing grounds.

In both fishing seasons, nearly all the recoveries occurred during the first three months of the season (e.g., Fig. 5).

Population structure

The mean CL (61.4mm, range 10.2–142.4mm) of lobsters caught in the Bay during 1985 was significantly smaller (z test, Hoel 1976; $z = 10.4$, $P<0.05$) than that of lobsters caught during 1986 (65.2mm,

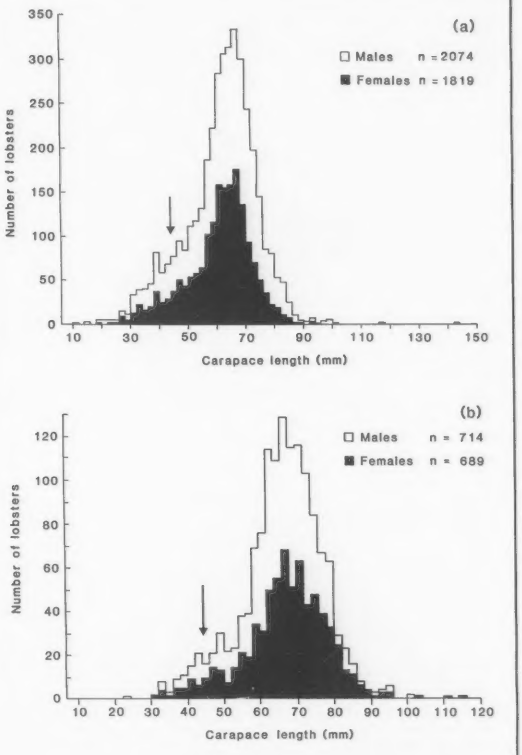


Figure 4
Size-frequency distribution of *Panulirus argus* caught in Bahía de la Ascensión for tagging purposes in (a) 1985 and (b) 1986. Tags were applied to lobsters ≥44 mm CL, as indicated by arrow.

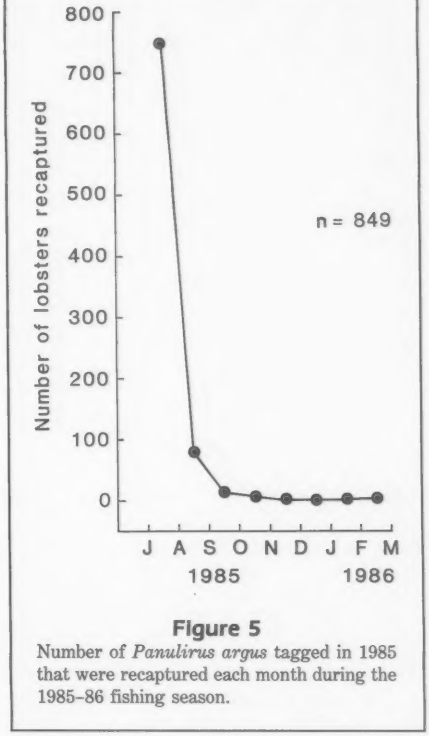


Figure 5
Number of *Panulirus argus* tagged in 1985 that were recaptured each month during the 1985–86 fishing season.

range 22.0 – 113.1 mm). However, the tagging operation in 1985 occurred one full month earlier than in 1986.

The means of CL of lobsters caught in each of the six sampling zones during 1985 and 1986 (Figs. 6, 7) were significantly different ($P<0.05$, approximate test of equality of means when the variances are heterogeneous; Sokal and Rohlf 1981, Box 13.2). An unplanned comparison among pairs of means (Sokal and Rohlf 1981) shows three groups of mean sizes in each year (Table 1). This result implies that the distribution of lobsters by size in the bay is not random. Smaller lobsters occupied the more interior of the six sampling zones (zones II, III, and IV), and larger lobsters occupied zones closer to the reef (zones I, V, and VI).

Growth and recruitment

Of the 849 lobsters recaptured during 1985–86 and the 407 recaptured during 1986–87, only 372 and 268, respectively, were returned with accurate CL information. All but two showed growth between tagging and recapture.

During the first three months of the 1985–86 season, the modal CL of recaptured males increased 10 mm. Growth of individuals was highly variable (Fig. 8) and in some cases indicates more than one molt occurred. For females (data not illustrated), the mode increased 8 mm.

Fabens' method (1965) for estimating growth parameters was used for both sexes and both years separately (Table 2a). The estimates of asymptotic length and the growth coefficient k by this method show great variability.

On the other hand, the EM algorithm needs some initial estimates before it can begin iterating, and the Fabens estimates were used for this. A set of data for males and females for each year was thus obtained (Table 2b). Combining the data over both years, for each sex, did not lead to a significant increase in the

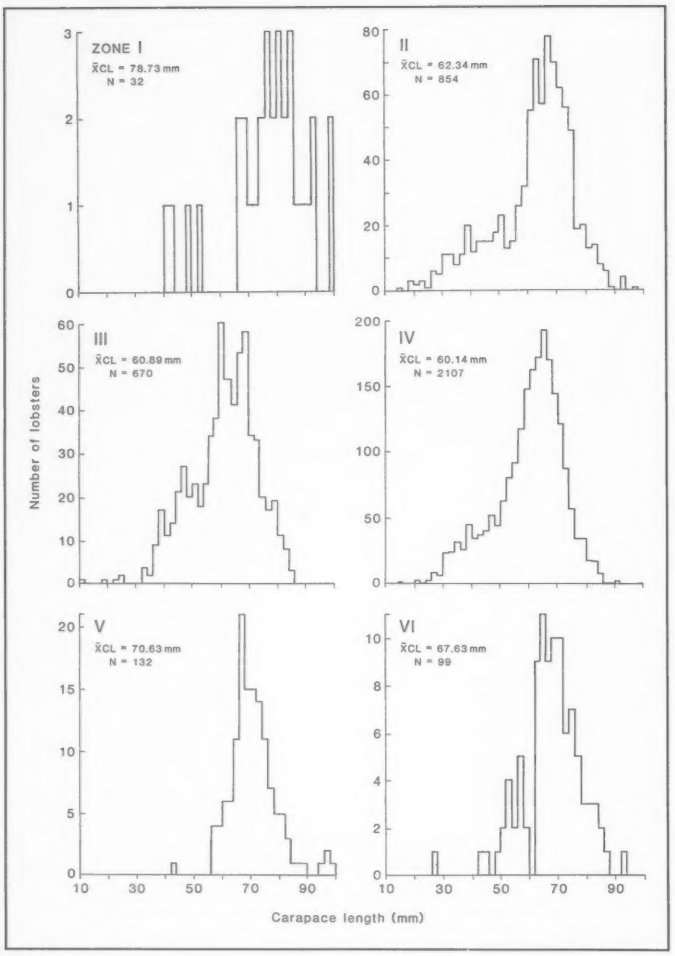


Figure 6
Size-frequency distribution of *Panulirus argus* caught in each sampling zone during the 1985 tagging operation in Bahía de la Ascensión.

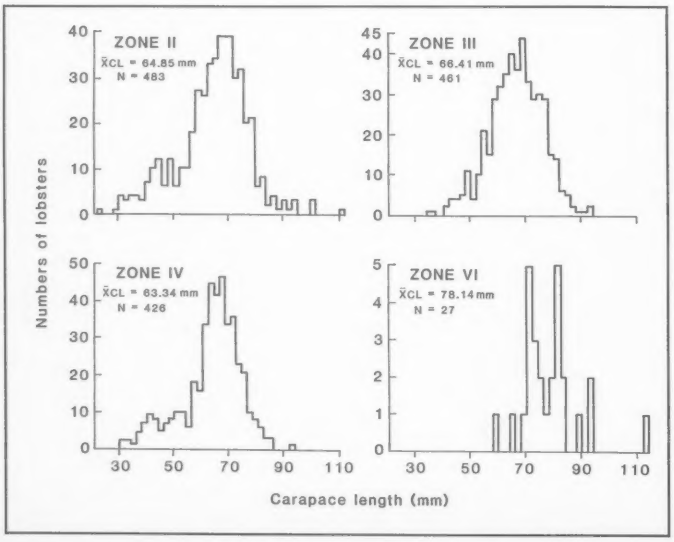


Figure 7
Size-frequency distribution of *Panulirus argus* caught in sampling zones II, III, IV, and VI during the 1986 tagging operation in Bahía de la Ascensión.

log-likelihood ratio, indicating that it was valid to pool the data over the two years, i.e., there was no difference in growth between years. However, combining the male and female data led to a significant increase in the log-likelihood ratio, indicating different growth rates for males and females. Males grew faster and larger than females, similar to other panulirid species (Kanciruk 1980). The final set of data is shown in Table 2c. Estimated mean growth curves for males and females, combined for both years, are shown in Figure 9.

The algorithm also predicts the age at which each animal was initially caught. The estimated non-parametric density function of age at first capture for the 1985 and 1986 data showed a clear mode around 525 days from settlement.

Growth of the lobsters in Bahía de la Ascensión was rapid. Males and females enter the fishery at 74 mm CL, 1.65 and 1.7 years, respectively, after settling. Allowing for a six-month larval period (Lewis 1951), males and females enter the fishery at approximately 2.15 and 2.2 years of age, respectively.

The analysis of mean weekly growth rates (Hunt and Lyons 1986) combining the 1985 and 1986 data (not illustrated) did not show any points of inflection, suggesting that there is no marked decrease in the growth rate of the lobsters in the bay.

Movements

Most of the recaptured lobsters were caught within the boundaries of the cooperative's fishing ground. Lobsters that

Table 1

Mean carapace length ($\bar{x}$ CL mm) of *Panulirus argus* caught in each of the six sampling zones. In 1986, no sampling was performed in zone I, and only five individuals were obtained in zone V. Mean CL's followed by corresponding letter in row are not significantly different ($P>0.05$). Means with different letter in row are significantly different ($P<0.05$), using test for unplanned comparisons among pairs of means.

	Zone					
	IV	III	II	VI	V	I
(a) 1985	60.14[a]	60.89[a]	62.34[a]	67.63[b]	70.63[b]	78.73[c]

	Zone			
	IV	II	III	VI
(b) 1986	63.34[a]	64.85[ab]	66.41[b]	78.14[c]

Table 2

Estimates of mean growth parameters for *Panulirus argus* form. $\hat{\Gamma}$ = dispersion matrix of the coefficients of the growth curve; $\hat{\sigma}^2$ = variability around an individual curve.

Ses	Year	L_∞	k
(a) Fabens' (1965) approach			
Males	1985	101.898	−0.0059
Males	1986	113.815	−0.0049
Females	1985	85.970	−0.0109
Females	1986	148.284	−0.0018
(b) Maximum likelihood approach (Palmer et al. 1988)			
Males	1985	255.464	−0.00057
Males	1985	261.501	−0.00054
Females	1985	222.807	−0.00065
Females	1986	218.149	−0.00067

$$\hat{\Gamma} = \begin{pmatrix} 10.295 & -0.00004 \\ & 2.16 \times 10^{-10} \end{pmatrix}$$

$$\hat{\sigma}^2 = 25.426$$

(c) Maximum likelihood approach (1985 and 1986 combined)			
Males		257.204	−0.00056
Females		215.605	−0.00068

$$\hat{\Gamma} = \begin{pmatrix} 10.349 & -0.000047 \\ & 2.19 \times 10^{-10} \end{pmatrix}$$

$$\hat{\sigma}^2 = 25.421$$

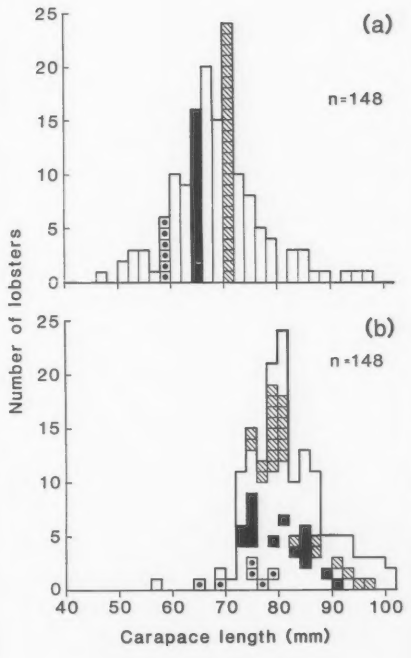


Figure 8

(a) Size at initial capture of 148 male *Panulirus argus* tagged at Bahía de la Ascensión, and (b) size of same males at recapture during first three months of 1985–86 fishing season. Shadings denote individual lobters and show carapace length increment by selected size cohorts, to emphasize variability in growth. It is possible that more than one molt is involved in some cases.

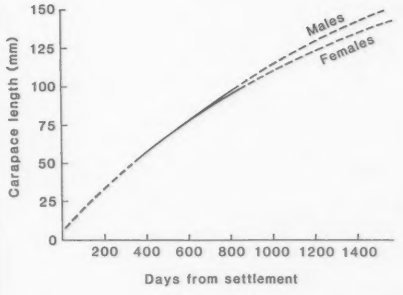


Figure 9

Growth curves for male and female *Panulirus argus*, as estimated by the maximum likelihood approach. Only the continuous lines are based on actual data; broken lines are extrapolations according to model.

dispersed from their zones of initial capture tended to move toward and along the reef in both years (Figs. 10, 11). As an example, of the 79 recaptured lobsters that had been tagged in zone III in 1985 (total number tagged in zone III = 581), 29 remained in zone III

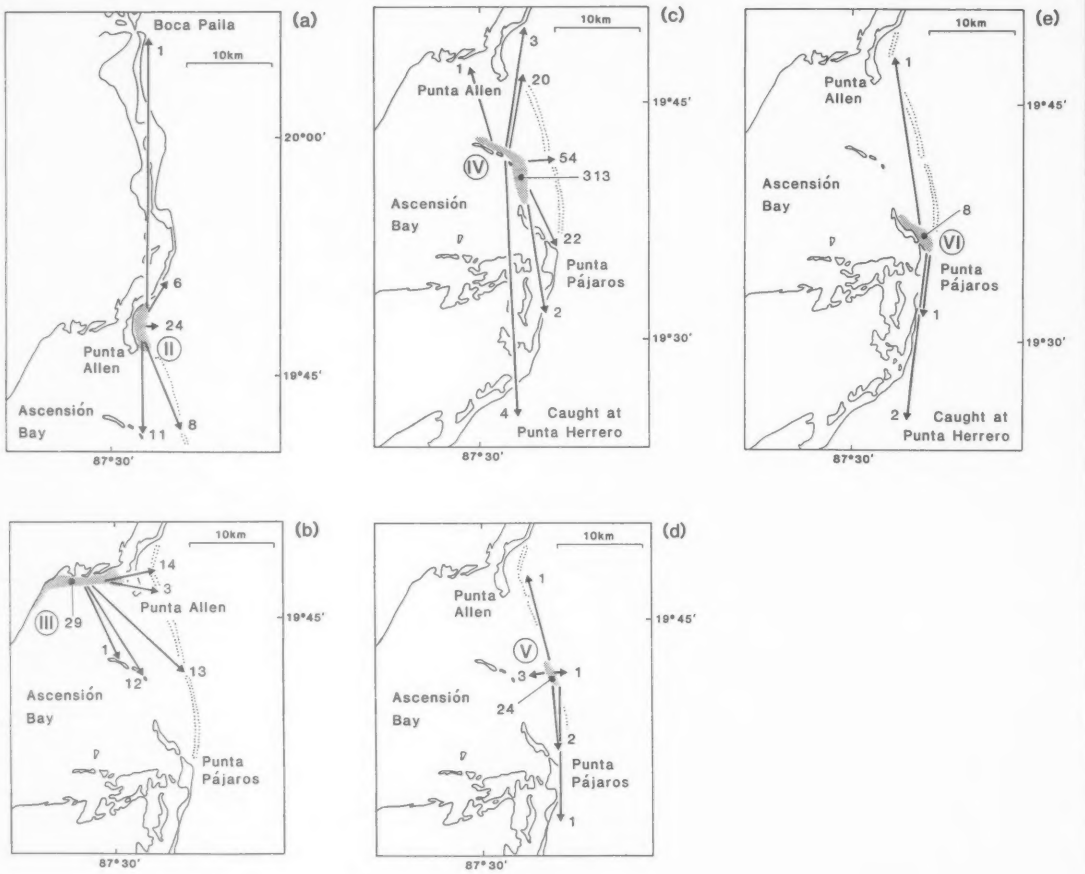


Figure 10

Recorded movements of *Panulirus argus* tagged in sampling zones II–VI in Bahía de la Ascensión, in 1985–86. Shaded areas denote sampling zones; arrows indicate direction of movements and arrowheads the sites of recapture. Numbers indicate lobsters that moved in each direction from denoted sampling zone.

and 42 moved to areas nearer or at the outer reef (Fig. 10b). However, because no lobster fishing was conducted in the inner half of the bay, no data have been obtained to indicate the possible movement of lobsters to that area.

In the 1985–86 fishing season, eleven lobsters were recaptured outside of the bay by fishermen of other cooperatives. Of these, ten had traveled south, while only one had gone north (Fig. 10). The longest straight-line distance traveled by an animal was 45 km. All the recaptured lobsters that were tagged in 1986 were caught in the fishing grounds of the cooperative "Pescadores de Vigía Chico." The longest distance traveled by any of these was 23 km (Fig. 11b).

No animals were caught north of Boca Paila or south of Punta Herrero (Fig. 10). However, fishing effort immediately outside the bay was restricted to skin diving on the reef to depths of about 15 m, so any lobsters that moved beyond that depth would not be recaptured.

Reproduction

During the 1985 tagging program, only four individuals (67.2, 82.5, 83.7, and 116.8 mm CL) of 1819 females had spermatophores attached, and only one individual (76.0 mm CL) carried eggs. In the 1986 program, five individuals (87.0, 90.2, 94.2, 94.9, and 100.3 mm CL)

of 689 females were found with remains of empty egg capsules and/or eroded spermatophores. In both years, all of the females that showed signs of reproductive activity were caught on the edge of the reef (zones II and V, Fig. 1b). No other evidence of reproductive activity was observed.

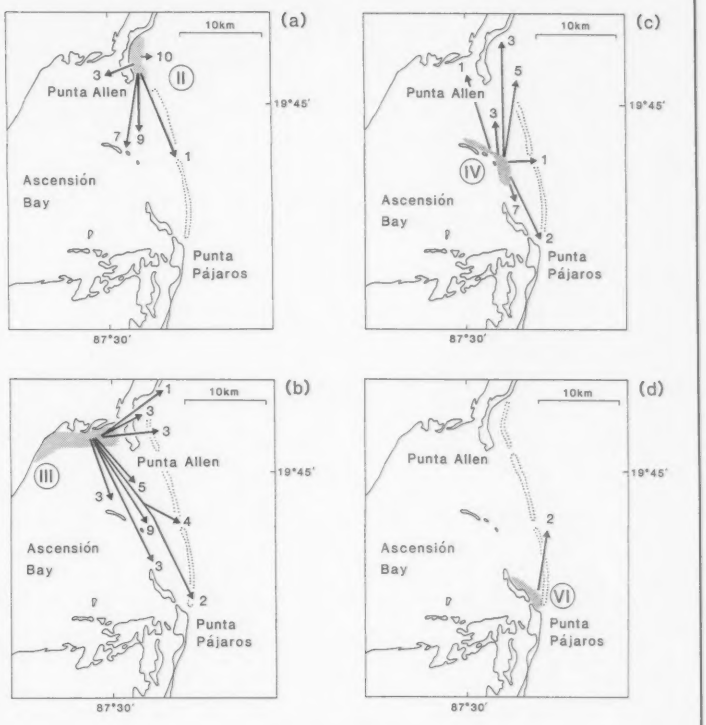


Figure 11

Recorded movements of *Panulirus argus* tagged in sampling zones II, III, IV, and VI in Bahía de la Ascensión, 1986–87. Shaded areas denote sampling zones; arrows indicate direction of movements and arrowheads the sites of recapture. Numbers indicate lobsters that moved in each direction from denoted sampling zone.

Discussion

A decline of CPUE from the beginning until the end of the fishing season has been reported for other *Panulirus argus* fisheries (Warner et al. 1977, Lyons et al. 1981). However, in the fishery of Bahía de la Ascensión, the decline from the first month of the season to the second is sharp. Eggleston et al. (1990) suggest that casitas enhance survivorship of juvenile lobsters by protecting them from their predators, hence increasing lobster production. Thus, during the closed season, in the absence of fishing mortality, it is possible that the aggregation effect of casitas on juvenile lobsters, in conjunction with recruitment by rapid growth, result in the catch from a casita being greater during the first month of the season than during the remainder of the season.

The high level of recaptures during both the 1985–86 and 1986–87 seasons suggests a high level of fishing mortality on the population in Bahía de la Ascensión. The failure to recapture any of the animals tagged in 1985 during the tagging program in 1986, and the fact that only four were recaptured during the fishing season in 1986–87, may reflect tag loss, high natural mortality, or a strong emigration from the bay. The latter is supported by the movements of the recaptured lobsters.

We could not separate fishing mortality from natural mortality because there appeared to be both recruitment by growth of small lobsters throughout the season as well as immigration onto the casitas from other areas. This is sustained by the monthly size composition of the catch by the fishery (Fig. 2). Those catches showed a nearly constant size distribution, with a mode near the minimum size limit, indicating recruitment by growth to the fishery throughout the fishing season.

The estimates of the growth parameters by the Fabens' method showed great variability (Table 2a), which could be interpreted in two ways: (1) Lobster growth differed greatly interanually, or (2) the procedure yielded unreliable estimates. Palmer et al. (1988) suggested that the Fabens method does not explicitly model individual variability in growth (e.g., Fig. 8), and that it produces inconsistent estimates of the asymptote of growth.

Alternatively, the maximum likelihood estimates of the mean curves did not show great variability, so both years could be pooled to obtain a final set of parameters. The reasonableness of the estimated parameters was further confirmed by the fact that *P. argus* can attain sizes much larger than the asymptotic sizes estimated from the Fabens method (Sutcliffe 1957, Munro 1974, Olsen and Koblic 1975, Farrugio 1975). However, the tagged lobsters were mostly juveniles and young adults as further demonstrated by the lack

of an inflection point in their mean weekly growth rate. Thus, the estimated parameters may reflect growth rates of immature lobsters only, and those of reproductive adults could change the last part of the curve (Fig. 9).

Lyons et al. (1981), utilizing a method that involved mean growth rates obtained from several authors, estimated an age of slightly more than two years after settlement as postlarvae for *P. argus* measuring 76 mm CL, allowing for a nine-month larval period. With our maximum likelihood results, and considering the same nine-month larval period, the estimated age for a 76 mm CL lobster would be 2.5 years. Munro (1974) produced a growth curve for *P. argus* based on data from 156 lobsters tagged and recaptured in Florida and Belize. His estimated age of one year after settling as postlarvae for lobsters measuring 45 mm CL agrees closely with the estimate obtained in the present study by the maximum likelihood approach. Peacock (1974) tentatively estimated an age of one year for 50 mm CL *P. argus*, as did Eldred et al. (1972) and Witham et al. (1968).

Therefore, the maximum likelihood approach utilized in this paper seems to have provided a useful set of growth parameters for juvenile and young adult *P. argus*, with the additional advantage of separating growth data between males and females.

The few signs of reproductive activity in female lobsters near the reef, in conjunction with small carapace length, indicated that the lobster population in Bahía de la Ascensión was probably composed mainly of juveniles. Lyons et al. (1981) found little evidence of mating activity of *P. argus* in the shallow Florida Keys, and they stressed that almost 90% of the spawning occurred at their reef and deep-water stations. Peacock (1974), Davis (1975), and Kanciruk and Herrnkind (1976) also reported an absence of reproductive activity in shallow bank or lagoon areas.

The movements demonstrated by the tagging program indicate a displacement of lobsters from shallows toward deeper habitats offshore. This was also supported by the analysis of the size composition by zones (Figs. 7, 8; Table 1), which indicated that the lobsters were smaller in the innermost sampling zones compared with those caught near or on the reef. Buesa (1970) and Cruz et al. (1986) suggested that juvenile *P. argus* in Cuba live in protected areas with seagrass beds and move towards the outer reefs as they grow. Other authors that mention similar movements for juvenile *P. argus* are Peacock (1974) in Barbuda, Olsen and Koblic (1975) in the U.S. Virgin Islands, Warner et al. (1977), Davis (1979), and Lyons et al. (1981) in Florida.

Although northern and southern movements were made by lobsters which left the bay, southerly movements predominated. In a three-year study of movements of *P. argus* in Biscayne Bay, Florida, Davis (1979) found southerly movements of tagged lobsters during the first year, northerly movements in the second year, and both northerly and southerly displacements during the third. He concluded that juvenile lobsters from Biscayne Bay are recruited into virtually the entire Florida fishery. The extent of the movements made through deeper water by the lobsters tagged in Bahía de la Ascensión—and their final destination—is still unknown, because from Tulum to Mahahual (Fig. 1a) lobsters are fished only in the bays and on the shallow parts of the reef. A winter migration, similar to that which occurs at the northeastern end of the Yucatán Península (Kanciruk and Herrnkind 1978), may take place in deeper waters outside the coral reef that runs across the front of the bay.

Small size, rapid growth, movements toward the reef areas, and lack of reproductive activity all serve as evidence that the population of lobsters in Bahía de la Ascensión is composed of juveniles. We hypothesize the existence of a population composed of reproductive adults off the coral banks of Bahía de la Ascensión, an area that is not currently being fished.

The existence of adult stocks outside of the bay and the output of lobsters from the bay into offshore deeper areas are issues that need to be assessed for future management plans. In addition, although casitas may provide critical refuge for juvenile lobsters from their natural predators (Eggleston et al. 1990), the long-term effects of the casitas on the lobster populations, as well as on the benthic communities associated with seagrasses and on the stability and structure of the seagrass beds themselves, remain to be determined through future field studies.

Acknowledgments

We acknowledge the field assistance of MariCarmen Martínez, Fernando Negrete, Gabriel Carrasco-Zanini, Alfredo Velázquez, Juan García, Edith Zárate, David Ortega, Carlos Rico, Alejandro Torres, and Jorge Simonín. The first three also helped with data processing. Mark Palmer, David Gutiérrez, Nick Caputi, and Norm Hall gave mathematical advice. William G. Lyons, Alan Campbell, and two anonymous reviewers greatly improved the manuscript. The study was supported by Universidad Nacional Autónoma de México, CSIRO-Australia, and Consejo Nacional de Ciencia y Tecnología de México (Joint Project No. 140134D202). Scientific fishing permits extended by the Fisheries Secretary of México made this study possible. We also express our thanks to the fishermen of the several cooperatives that assisted the study, particularly the "Pescadores de Vigía Chico."

Citations

Buesa, R.J.
1970 Migraciones de la langosta (*Panulirus argus*). Mar Pesca 60:22–27 [in Spanish].

Chittleborough, R.G.
1974 Development of a tag for the western rock lobster. CSIRO Div. Fish. Oceanogr. Rep. 56:1–19.

Cruz, R., R. Brito, E. Diaz, and R. Lalana
1986 Ecología de la langosta (*Panulirus argus*) al SE de la Isla de la Juventud. II. Patrones de Movimiento. Rev. Invest. Mar. 7(3):19–35 [in Spanish, Engl. abstr.].

Davis, G.E.
1975 Minimum size of mature spiny lobsters, *Panulirus argus*, at Dry Tortugas, Florida. Trans. Am. Fish. Soc. 104:675–675.
1979 Management recommendations for juvenile spiny lobsters, *Panulirus argus*, in Biscayne National Monument, Florida. South Fla. Res. Cent. Rep. M-530, Homestead, FL 33030, 32 p.

Dempster, A.P., N.M. Laird, and D.B. Rubin
1977 Maximum likelihood from incomplete data via the EM algorithm (with discussion). J. R. Stat. Soc. Ser. 39:1–38.

Eggleston, D.B., R.N. Lipcius, D.L. Miller, and L. Coba-Cetina
1990 Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. Mar. Ecol. Prog. Ser. 62: 79–88.

Eldred, B., C.R. Futch, and R.M. Ingle
1972 Studies of juvenile spiny lobsters, *Panulirus argus*, in Biscayne Bay, Florida. Fla. Dep. Nat. Resour. Mar. Res. Lab., Spec. Sci. Rep. 35, 15 p.

Fabens, A.J.
1965 Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289.

Farrugio, H.
1975 Observations sur deux langoustes de la Martinique: *Panulirus argus* et *Panulirus guttatus*; premières données biométriques et étude comparée de leurs croissances rélatives. Sci. Pêche, Bull. Inst. Pêches Mar. 240:11–20 [in French].

Hoel, P.G.
1976 Elementary statistics. John Wiley, NY, 361 p.

Hunt, J.H., and W.G. Lyons
1986 Factors affecting growth and maturation of spiny lobsters, *Panulirus argus*, in the Florida Keys. Can. J. Fish. Aquat. Sci. 43:2243–2247.

Jordan, E.
1988 Estudio regional de los arrecifes coralinos del Mar Caribe mexicano: Su potencial de uso. Informe Final, Proyecto PCCNA-021928, Inst. Cienc. del Mar y Limnol Univ. Nal. Autón. México/Consejo Nal. Cienc. y Tecnología [in Spanish].

Kanciruk, P.
1980 Ecology of juvenile and adult Palinuridae (spiny lobsters). *In* Cobb, J.S., and B.F. Phillips (eds.), The biology and management of lobsters, vol. II, p. 59–96. Academic Press, NY.

Kanciruk, P., and W.F. Herrnkind
1976 Autumnal reproduction in *Panulirus argus* at Bimini, Bahamas. Bull. Mar. Sci. 26:417–432.
1978 Mass migration of spiny lobsters, *Panulirus argus* (Crustacea: Palinuridae): Behavior and environmental correlates. Bull. Mar. Sci. 28:601–623.

Laird, N.M., N. Lange, and D. Stram
1987 Maximum likelihood computations with repeated measures: Application of the EM algorithm. J. Am. Stat. Assoc. 82:97–105.

Leslie, P.H., and D.H.S. Davis
1939 An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 8:94–113.

Lewis, J.B.
1951 The phyllosoma larvae of the spiny lobster *Panulirus argus*. Bull. Mar. Sci. Gulf Caribb. 1(1):89–103.

Lozano, E., P. Briones, and B.F. Phillips
1989 Spiny lobster fishery at Bahía de la Ascensión, Q.R. *In* Chávez, E. (ed.), Proc., Workshop Australia-Mexico on marine sciences, Mérida, México, July 1987, p. 379–391. Centro de Invest. Estudios Avanzados, Merida 97310, Mexico.

Lyons, W.G., D.G. Barber, S.M. Foster, F.S. Kennedy Jr., and G.R. Milano
1981 The spiny lobster, *Panulirus argus*, in the middle and upper Florida Keys: Population structure, seasonal dynamics and reproduction. Fla. Mar. Res. Publ. 38, 38 p.

Miller, D.L.
1982 Construction of shallow water habitat to increase lobster production in Mexico. Proc. Gulf Caribb. Fish. Inst. 34: 169–179.

Munro, J.L.
1974 The biology, ecology, exploitation and management of Caribbean reef fishes. Part V.1.—The biology, ecology and bionomics of Caribbean reef fishes: Crustaceans (Spiny lobsters and crabs). Res. Rep. 3, Zool. Dep., Univ. West Indies, Kingston, Jamaica, 57 p.

Olsen, D.A., and I.G. Koblic
1975 Population dynamics, ecology and behavior of spiny lobster, *Panulirus argus*, of St. John, USVI. II. Growth and mortality. Nat. Hist. Mus. Los Angel. Cty. Sci. Bull. 20:17–22.

Palmer, M.J.
1986 Calibration of noisy scrub bird with repeated measurements. CSIRO Div. Math. Stat. Consult. Rep. WA(C) 86/3, Floreat Park, W.A. 6014, Australia.

Palmer, M.J., B.F. Phillips, and G.T. Smith
1988 Application of random coefficient models to capture-recapture data. Submitted to Biometrics.

Peacock, N.A.
1974 A study of the spiny lobster fishery of Antigua and Barbuda. Proc. Gulf. Caribb. Fish. Inst. 26:117–130.

Secretaría de Pesca
1987 Pesquerias Mexicanas: Estrategias para su administración. Dir. Gral. Admin. de Pesquerías, Secretaría de Pesca, Alvaro Obregón 269, México, D.F., 1061 p. [in Spanish].

Sokal, R.R., and F.J. Rohlf
1981 Biometry. W.H. Freeman, San Francisco, 859 p.

Sutcliffe, W.H. Jr.
1957 Observations on the growth rate of the immature Bermuda spiny lobster, *Panulirus argus*. Ecology 38:526–529.

Warner, R.E., C.L. Combs, and D.R. Gregory Jr.
1977 Biological studies of the spiny lobster, *Panulirus argus* (Decapoda: Palinuridae) in south Florida. Proc. Gulf Caribb. Fish. Inst. 29:166–183.

Witham, R., R.M. Ingle, and E.A. Joyce Jr.
1968 Physiological and ecological studies of *Panulirus argus* from the St. Lucie Estuary. Fla. Board Conserv. Mar. Res. Lab. Tech. Ser. 53:1–31.

Comparison of Two Techniques for Estimating Tilefish, Yellowedge Grouper, and Other Deepwater Fish Populations

Gary C. Matlock
Fisheries Division, Texas Parks and Wildlife Department
4200 Smith School Road, Austin, Texas 78744

Walter R. Nelson
Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA
75 Virginia Beach Drive, Miami, Florida 33149

Robert S. Jones
Marine Science Institute, University of Texas at Austin
P.O. Box 1267, Port Aransas, Texas 78373

Albert W. Green
Environment Assessment, Texas Parks and Wildlife Department
4200 Smith School Road, Austin, Texas 78744

Terry J. Cody
Coastal Fisheries Branch, Texas Parks and Wildlife Department
100 Navigational Circle, Rockport, Texas 78382

Elmer Gutherz
Mississippi Laboratory, National Marine Fisheries Service, NOAA
P.O. Drawer 1207, Pascagoula, Mississippi 39567

Jeff Doerzbacher
11505 Oak Branch Drive, Austin, Texas 78737

Abstract.–Tilefish *Lopholatilus chamaeleonticeps* and yellowedge grouper *Epinephelus flavolimbatus* are deepwater fishes and targets of a relatively recent bottom longline fishery in the Gulf of Mexico. They are long-lived, slow growing, have very limited movements and distribution, and are susceptible to longlines. However, population size and life-history parameter estimates are generally unknown for Gulf fish. This study compared two methods for estimating population sizes to determine the most cost-effective one for use on long-term fishery-independent stock assessments. Bottom longlines were used to deplete fish from a small area, and a regression of catch per effort on cumulative catch was used to estimate the area's population prior to fishing. The population was also estimated by counting fish burrows from a submersible and expanding the mean number per unit area by the study site's area after correcting for the number of occupied burrows. Longlines and submersibles provided significantly different estimates of tilefish populations, the only species for which estimates could be compared. Longline estimates were probably more accurate because errors in area estimation and double counting were evident in submersible data. Longlines were less expensive to operate ($5000 vs. $8000 per day) and they afforded collection of size, age, and sex data on each fish caught. These data were not available from the submersible. Longlines could be used more cost-effectively than submersibles in determining long-term population changes. However, direct observation of fish behavior was not available from longlines, but was from the submersible. Submersibles also provide data on habitat and gear assessment, including deployment, efficiency, bait predation, and potential catch loss during retrieval.

Manuscript accepted 1 August 1990.
Fishery Bulletin, U.S. 89:91–99 (1991).

Tilefish *Lopholatilus chamaeleonticeps* support an economically important bottom longline fishery in the Mid-Atlantic Bight (Grimes et al. 1980, Turner 1986), and are the focus of a developing longline fishery in the South Atlantic Bight and the Gulf of Mexico (Katz et al. 1983, Low et al. 1983). Impacts of this development in the Gulf are unknown because population sizes and life-history parameter estimates there are generally unknown. However, the potential for recruitment overfishing appears large even at relatively low fishing effort because of the fish's life history (Harris and Grossman 1985). The fish is long-lived, slow growing (Turner et al. 1983, Harris and Grossman 1985), has limited movement (Grimes et al. 1983, 1986), and is restricted to temperatures of 9–14°C (Grimes et al. 1986, Freeman and Turner 1977). Tilefish are burrowers, requiring a clay substrate that is soft enough to allow burrowing, but firm enough for maintenance of burrows that may exceed 1 m in diameter and 3 m in depth (Able et al. 1982, Grimes et al. 1986, Twichell et al. 1985). In the Gulf of Mexico this is a narrow geographic area along the outer edge of the continental shelf between depths of 229 and 411 m (Nelson and Carpenter

1968, Wolf and Rathjen 1974). For the above reasons, tilefish are susceptible to capture on longlines (Nelson and Carpenter 1968, Wolf and Rathjen 1974, Grimes et al. 1982, Cody et al. 1981) and overfishing (Harris and Grossman 1985).

Yellowedge grouper *Epinephelus flavolimbatus* are also a target of the developing Gulf longline commercial fishery (Prytherch 1983, Graham 1978). However, even less is known about the life history and populations of this species than of tilefish. They are apparently present in commercial concentrations off Texas in the 128–274 m depth zone (Nelson and Carpenter 1968). On only 90 trips in the Gulf in 1982 over 65,000 kg of yellowedge grouper were landed (Prytherch 1983). However, their frequent distribution around rock and coral formations may preclude sustained commercial catches because of gear loss (Graham 1978).

This study was conducted to contrast "fishing out" an area with bottom longlines to direct visual observations from a small research submersible as methods for determining population sizes of tilefish, yellowedge grouper, and other deepwater fishes. The impact of longline fishing on these populations within a limited area was also determined.

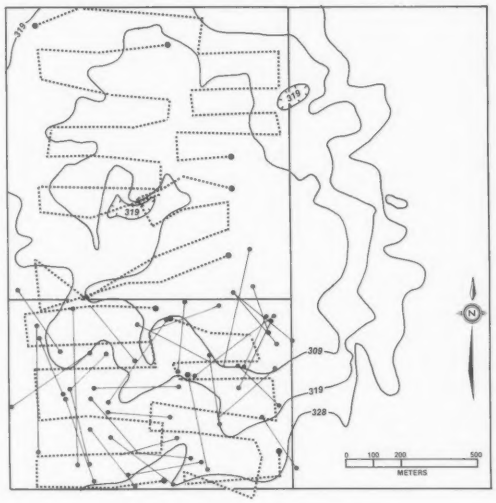


Figure 1
Tilefish study area (center point at 27°40.0′N lat. and 94°22.8′W long.) showing depth contours in meters, submersible transect tracks (dashed lines), and distribution of longline sets (solid lines) within the southern part of the study area. Chart represents one square nautical mile.

Materials and methods

Preliminary activities

In May 1984 the NOAA ship *Oregon II* spent 6 days surveying an area measuring 95 km east-to-west (94° 10′ long. to 95°00′W long.) between 183- and 457-m depths directly south of Galveston, Texas. Bottom configuration and acoustic signatures of fish were noted with a color-enhanced fathometer. Eleven bottom longline sets were made during each day to locate areas of high tilefish and yellowedge grouper catch rates (≥0.3 fish/100 hook-hours). Based on these preliminary cruises, specific sites were chosen for the submersible and longline studies described in this paper. Three days (10–13 September 1984) were spent by the *Oregon II* making detailed charts of each study site prior to the arrival of the submersible. Bathymetric charts of each site were developed using a depth sounder and Loran "C" plotter. These charts represented an area 2.6 km^2 (1 nmi^2) and were contoured by 10-m depth intervals. The trackline interval used in mapping was about one track per 15 m. The charts were duplicated and copies were provided to the Harbor Branch Foundation's RV *Johnson* prior to the beginning of submersible and fishing activities. This allowed both vessels to track and plot the position of the submersible and location of longline sets precisely.

Study area

Tilefish A study area (1.9 × 1.1 km) was selected off the north Texas coast at 27°40.0′N lat. and 94°22.8′W long. (Fig. 1). The area was a broad ridge with a minimum depth of 304 m. Approximately 50% of the study area was less than 311 m in depth with the bottom dropping gradually away to 316–318 m at the northern part of the area, and 320–329 m in the southwestern part. The area was almost entirely covered with a soft sand-clay mixture, characteristic of tilefish habitat along the entire U. S. eastern coastline (Freeman and Turner 1977, Able et al. 1982, Twichell et al. 1985, Grimes et al. 1986). However, the substratum was less cohesive than in east coast tilefish grounds. A fin-stabilized metal rod, dropped from a height of 1.2 m by the submersible's manipulator arm, penetrated 80–100 cm in the gulf and 20–30 cm on east coast tilefish grounds (C.B. Grimes et al., NMFS Panama City Lab., unpubl. data for Mid-Atlantic Bight and South Atlantic off Florida).

Many of the burrows in the study area were dug at an oblique angle into the substratum or into a sloping face, instead of perpendicular as is characteristic of east coast tilefish on flat bottom (Able et al. 1982, Grimes et al. 1986). It was evident that the low cohesiveness

of the sediment probably caused the frequently observed cave-ins and sloughing of sediment around the mouths of burrows. Extensive secondary bioerosion by galatheid crabs and other burrowers (similar to the mechanism described by Able et al. 1982 and Grimes et al. 1986) further weakens the structure, contributing to cave-ins of the burrow roofs dug at an angle. Consequently, large areas of up to 6 × 9 m appeared to be plowed or cratered. It is not known if these broad areas were caused by one or several tilefish within each of the "plowed areas," or if one or more generations of tilefish were responsible.

Other tilefish burrows found in the study site were more like the typical "vertical" burrows known for these animals (Able et al. 1982, Grimes et al. 1986). Vertical burrows are apparently more stable than oblique ones, requiring less constant re- excavation. Some burrows that had become inactive were filled with sediment at the shaft entrance, but they showed evidence of recent bioerosion around their margins from secondary burrowers. There were also extensive areas that contained numerous depressions, apparently remains of old structures that were 1–2 m across and 0.6–1.5 m deep. Concentrations of 15–20 such depressions, 6–8 filled-in burrows, and 2–5 active burrows were common in the study area.

Yellowedge grouper A study area (1.28 × 1.28 km) slightly inshore of the tilefish site was selected at 27°41.3′N lat. and 94°23.6′W long. (Fig. 2). Depth ranged from 267 m along a central ridge to 311 m at the outer edge of the study area. The area was characterized by isolated boulders and scattered low rock ridges concentrated in depths of less than 283 m. The bottom was comprised of a sand-clay mixture interspersed with rubble and shell. Patches of avalanche anemones (*Bolocera* sp.) and sea pens (*Penatula* sp.) were frequently attached in the vicinity of rubble and "hard bottom." Bottom temperature fluctuated little at the study site (12.0–12.9°C). Fishing activities were confined to a 640 × 640 m (409,600 m^2) quadrant of the study area because time available was shortened by bad weather.

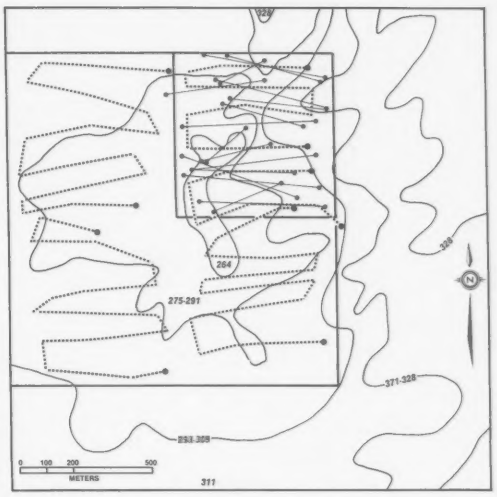


Figure 2
Yellowedge grouper study site (center point at 27°41.3′N lat. and 94°23.6′W long.) showing depth contours in meters, submersible transect tracks (dashed lines), and distribution of longline sets (solid lines) within the northeast part of the study area. Chart represents one square nautical mile.

Study activities

Submersible observations Burrow and fish counts were made from the submersible *Johnson-Sea-Link* during morning. Accordian-type transects with randomly selected starting points and alternating 366 (east–west) and 91-m (north–south) legs (up to 2652 m total distance per dive) were run with the submersible within 1 m of the bottom and traveling at 1.9 km/h. At the end of the east–west portions of each transect leg, the submersible would maintain position while the RV *Johnson* maneuvered directly above and recorded the position on a LORAN plot of the study area. Five transect dives were made on each of the study areas (Figs. 1, 2). Two of these transects were located completely within the portions of the tilefish area fished with longlines; one transect was completely within the fished portion of the grouper area.

The number of adult and juvenile burrows that were "filled-in" (denoting previous occupancy) or were "depressions" (characteristic of long-abandoned burrows that had been gradually filled in and smoothed over) were counted as inactive burrows. All others were counted as "active" (currently used by fish); only "active" burrow counts were used in estimating populations. Burrows within 7.3 m on either side of the submersible in the tilefish area and 11.0 m in the yellowedge grouper area were counted. These viewing distances were based on the range of visibility and viewing angles and were different in the two study areas because grouper and their burrows were generally larger than tilefish. So, grouper could be seen farther away than tilefish. All tilefish and yellowedge grouper seen were counted. All other fish seen were identified to species, if possible (names follow Robins et al. 1980), and these identifications were verified

using photographic and video records made during each dive.

Occupancy of "active" burrows was estimated by observing tilefish diving into burrows and by observing "smoking" (sediment plumes extruded) burrows during each of three other dives. These "positive" sightings provided a minimum estimate of occupancy of the total number of active-looking burrows seen on each dive. Occupancy dives were not conducted in the yellowedge grouper site, because grouper were usually seen outside their burrows and only moved out of sight into burrows when the submersible approached.

Bottom longline fishing Intensive fishing activities were conducted with bottom longlines in a portion of each study area (Figs. 1, 2). In the tilefish area longline sets consisted of 100 No. 7 circle hooks on 4.6-cm gangions, attached to a 366-m long ground line with halibut line snaps. Weights were used at both ends of the longline to prevent movement of the line along the bottom. Longlines were baited with squid and fished during daylight only. Two lines were fished on a rotating basis, with sets being soaked for approximately 2 hours. A maximum of eight sets (800 hooks) were made per day. In the yellowedge grouper area "Kali" poles were used to reduce gear loss caused by hanging on large boulders. This gear consisted of 40 2.4-m long PVC pipes weighted at one end and buoyed at the other, with 5 hooks 20.3 cm apart on each pole separated vertically by about 0.5 m. One pole was clipped to a floating mainline every 9 m with a halibut line snap. The "Kali" lines had only the lower end of the PVC pipe and anchors touching bottom. The lines were set at randomly selected locations for approximately 2 hours, using squid for bait.

Upon retrieval of all longlines, number of hooks returned, number of baits returned, and catch by species were recorded. Catch-per-unit-effort (CPUE) was calculated for each set using number of hooks returned.

Data analysis

Population densities and sizes were estimated using the Leslie method modified by Braaten (Ricker 1975, p. 151) from longline catches of Cuban dogfish *Squalus cubensis*, gulf hake *Urophycis cirrata*, southern hake *U. floridana*, and tilefish in the longline-fished portion of the tilefish area; and barrelfish *Hyperoglyphe perciformis*, longspine scorpionfish *Pontinus longispinis*, southern hake, and yellowedge grouper in the longline-fished portion of the grouper area. A regression of CPUE (in number of fish/100 hook-hours) for each longline on adjusted (50% of each day's total catch) cumulative daily catch was calculated using least squares regression weighted by the inverse of variance in daily CPUE (SAS 1982). The cumulative catch was adjusted to reduce bias that can result from using the cumulative catch at the start or end of each fishing period (Braaten 1969). The X-axis intercept was the population estimate ($\hat{N}$) for the area fished. Associated 95% confidence intervals were calculated following Sokal and Rohlf (1981, p. 498). Catchability coefficients (for species caught on longlines with significant regressions) were equal to the slopes of the regressions (Ricker 1975, p. 150). The assumptions of this technique include constant catchability, geographically closed (within the study area) population (i.e. no recruitment or emigration), no natural mortality, and constant fishing effort (Ricker 1975).

Data from the submersible were used to estimate tilefish and yellowedge grouper populations ($\hat{N}$) within the area fished with longlines (fished) and the remaining portion of the study area (unfished). There were two transects made in the fished portion, and three transects in the unfished portion of the tilefish study area. There was one transect made completely in the fished portion, and four transects in the unfished portion of the yellowedge grouper study area. These populations were estimated as the product of the mean number of burrows or fish per km^2, the percent burrow occupancy (for tilefish only), and the total km^2 in the study area. The mean number of burrows or fish per km^2 ($\pm$ 1 SE) was estimated for each transect and each area using the mean and variance equations for the delta-distribution (Pennington 1983, 1986) after transforming the density data along each leg of each transect to natural logarithm. Differences in mean densities were tested using the t-test (Sokal and Rohlf 1981). Occupancy was estimated as the mean percent ($\pm$ 1 SE) from three dives using the "smoking" burrow data discussed previously using the ratio estimator (Cochran 1977). The variance of the population estimates ($\hat{N}$) based on burrow counts was calculated as the variance of a product (burrows/km^2 $\times$ percent occupancy; Goodman 1960). Differences in the population estimates resulting from the longlines and submersibles were tested using the t-test (Cochran 1977, Sokal and Rohlf 1981) and variances associated with the population estimates.

Results

Fish data from longlines and submersibles provided significantly different estimates of tilefish populations. Population estimates for yellowedge grouper could not be made from the longline data because it did not yield a significant regression (Table 1). The number of tilefish (with 95% confidence intervals in parentheses) in the

Table 1

Population estimates and 95% confidence intervals (CI) for fishes caught on longlines and observed during submersible dives on the tilefish and grouper study areas off Galveston, Texas during September 1984. Longline estimates for fishes other than tilefish and yellowedge grouper were made only for species with significant relationships between catch-per-unit-effort and cumulative catch (Ricker 1975). Submersible estimates were based on expansions of mean burrows or fish per unit area seen on one and two transects in the grouper and tilefish study sites, respectively, to the total fished area (836,067 m^2).

	Longline					Submersible		
Species	No. of days	Y-intercept (± 1 SE)	Slope (± 1 SE)	R^2	F	N (95% CI)	No. of transects	N (95% CI) based on burrows	N (95% CI) based on fish seen
Tilefish site									
Tilefish	7	4.026 ± 0.835	−0.050 ± 0.012	0.382	18.574**	81 (39–128)	2	446(364–522)[a]	134(121–147)
Cuban dogfish	7	5.410 ± 1.190	−0.084 ± 0.020	0.371	17.677**	65 (24–108)			
Gulf hake	7	0.491 ± 0.330	−0.005 ± 0.010	0.007	0.209NS				
Southern hake	7	1.874 ± 0.501	−0.043 ± 0.013	0.260	10.554**	43(−27–121)			
Grouper site									
Yellowedge grouper	3	0.914 ± 0.383	−0.030 ± 0.020	0.140	2.277NS		1	150(105–195)	150(118–182)
Southern hake	3	3.445 ± 1.154	−0.052 ± 0.020	0.320	6.587*	66 (9–170)			
Longspine scorpionfish	3	0.995 ± 0.287	−0.013 ± 0.013	0.066	0.983NS				
Barrelfish	3	1.713 ± 0.705	−0.027 ± 0.017	0.157	2.605NS				

[a]Mean percent occupancy of burrows was 35.6 ± 16.8 (95% CI).

fished portion of the study area was 81 (39–128) based on longline catches; the estimate from submersible data was 134 (121–147) based on observed fish (Table 1). These estimates were significantly different from each other ($t = 4.939$, df = 29, $P<0.05$). The estimated number of tilefish based on burrow counts (446, 364–522) was four to five times higher than either of the fish-based estimates. The estimated number of yellowedge grouper in the fished portion of the grouper area was 150 (118–182) fish based on submersible grouper data and 150 (105–195) based on burrow data (Table 1). Again, no comparable estimate was made from longline data.

The estimated number of tilefish seen per unit area was significantly ($t = 3.621$, df = 51, $P<0.05$) greater (about 30%) in the fished area than in the unfished portion of the study area. There were also significantly ($t = 5.899$, df = 42, $P<0.05$) more yellowedge grouper (about 68%) seen in the fished area than in the unfished area (Table 2). This same pattern was apparent in the burrow data for tilefish ($t = 3.737$, df = 51, $P<0.05$) and yellowedge grouper ($t = 6.381$, df = 42, $P<0.05$). In the unfished portion of the grouper study area, the mean number of yellowedge grouper burrows seen per km^2 (70, 95% CI = 62–78) was less than 50% of the mean number of yellowedge grouper seen (170, 95% CI = 154–186) (Table 2). However, the number of burrows seen in the tilefish study area in both the fished and unfished portions exceeded the number of tilefish seen by about 10 to 20 times.

Estimates using submersible data could not be made for southern hake, gulf hake, Cuban dogfish, longspine scorpionfish, and barrelfish since they were generally not seen from the submersible. However, longlines caught 322 of these fishes during the 12,000–13,000 hook-hours of fishing on the tilefish and grouper study areas. Longline catch rates declined through time for southern hake in both study areas and Cuban dogfish caught in the tilefish study area, but no significant change in catch rates was detected for gulf hake in the tilefish study area or longspine scorpionfish or barrelfish in the grouper study area. Therefore, population estimates and 95% confidence intervals were only made for southern hake and Cuban dogfish; 43 (−27–121) and 65 (24–108) fish, respectively, in the tilefish study area and 66 (9–170) southern hake in the grouper study area (Table 1). More species were seen from the submersible than were caught on longlines (Table 3), but more population estimates could be made from longline data than from submersible data.

Table 2

Mean number of tilefish and yellowedge grouper and burrows of each species seen per km^2 on transects by a submersible in areas fished with longlines (study sites) and adjacent areas. Mean number of tilefish burrows seen was multiplied by mean percent occupancy (0.36 ± 0.16) to estimate number of tilefish and grouper. Width of each transect was 14.6 and 22.0 m for tilefish and grouper areas, respectively. The number of transect legs (n) is indicated for each transect.

	Tilefish						Yellowedge grouper					
			Fish		Burrows				Fish		Burrows	
Area	Transect	n	$\bar{x}$	SE	$\bar{x}$	SE	Transect	n	$\bar{x}$	SE	$\bar{x}$	SE
Fished with longlines	A	11	109	24	1500	80	F	11	370	30	370	50
	B	13	150	29	1400	80						
	Pooled	24	134	13	1500	40						
Adjacent (unfished)	C	7	12	5	900	300	G	11	70	9	60	8
	D	11	109	19	900	40	H	11	300	30	120	20
	E	11	150	19	3400	70	I	11	100	20	50	9
	Pooled	29	100	7	1700	60	Pooled	33	170	8	70	4
Pooled		53	117	3	1600	30		44	220	7	140	6

Table 3

List of species caught on longlines and seen from submersible in the tilefish and grouper study areas. An X indicates presence; blank indicates absence.

Common name	Scientific name	Longline	Submersible
Tilefish	*Lopholatilus chamaeleonticeps*	x	x
Yellowedge grouper	*Epinephelus flavolimbatus*	x	x
Southern hake	*Urophycis floridana*	x	x
Gulf hake	*Urophycis cirrata*	x	
Cuban dogfish	*Squalus cubensis*	x	x
Longspine scorpionfish	*Pontinus longspinus*	x	x
Barrelfish	*Hyperoglyphe perciformis*	x	x
Night shark	*Carcharhinus signatus*	x	
Chain dogfish	*Scyliorhinus retifer*	x	x
Chub mackerel	*Scomber japonicus*	x	
Snowy grouper	*Epinephelus niveatus*	x	x
Beardfish	*Polymixia lowei*	x	x
Moray	*Gymnothorax kolpos*	x	x
Conger eel	*Conger oceanicus*		x
Argentines	*Argentine* sp.		x
Shortnose greeneye	*Chlorophthalmus agassizi*		x
Reticulate goosefish	*Lophiodes reticulatus*		x
Red hake	*Urophycis chuss*		x
Buckler dory	*Zenopsis conchifera*		x
Slimehead	*Gephroberyx darwini*		x
Deepbody boarfish	*Antigonia capros*		x
Longspine snipefish	*Macrorhamphosus scolopax*		x
Longtail bass	*Hemanthias leptus*		x
Yellowfin bass	*Anthias nicholsi*		x
Bladefin bass	*Jeboehlkia gladifer*		x
	Polylepion n sp.		x
Flatheads	*Bembrops* sp.		x
Scorpionfish	*Scorpanenodes* sp.		x

Discussion

Longlines appear to be a more cost-effective means of monitoring fish population changes than submersibles. However, longlines kill all the collected fish whereas submersibles do not. More data can be collected on each caught fish at a lower cost with longlines than with a submersible. Size, age, and sex data could be collected from longline catches at a cost of about $5000 per day (in 1984 U.S. dollars), while none of these data were available from the submersible even though it cost about $8000 per day to operate. Additionally, the tilefish population based on burrow data from the submersible may have been overestimated because (1) "active" burrows were overestimated, (2) width of each burrow-count transect was underestimated, and (3) double counting occurred when transects crossed or came close to crossing. The number of tilefish estimated from tilefish seen was about 50% larger than the estimate based on longlines, and was about four times less than the estimate based on burrow counts. The number of burrows may be more a reflection of population size prior to exploitation if this area was heavily fished prior to our study.

Tilefish populations were probably underestimated using longline data. But the amount of bias is unknown. Capture probabilities were not constant, and this usually leads to underestimates (White et al. 1982). Recruit-

ment and emigration rates are unknown, but were probably low. If they occurred, recruitment must have been less than emigration because the populations were depleted in the study area. As recommended by Ricker (1975), our fishing effort was concentrated into "a rather short period of time" to minimize the effects of violating this assumption and that of no natural mortality.

The grouper population based on submersible fish data may have been overestimated because the estimated number of fish exceeded the estimated number of burrows and double counting of fish probably occurred. On one dive, the same fish (based on a scar on the lower jaw) was seen four different times.

Additional research is needed to determine the impacts of each of the above factors on fish population estimates based on counts made from submersibles. Future burrow counts should include all burrows, not just apparently active ones. Transect width should be accurately measured by counting burrows only within the range of a fixed physical extension from the submersible. Occupancy rates for tilefish and yellowedge grouper should be determined in randomly selected areas at night when they are most likely to be in their burrows.

Although no significant relationship between CPUE and cumulative catch was found for grouper, a more intensive effort should be made before discounting this technique. Additional longline collections over a longer period for yellowedge grouper are needed to determine if using the Leslie method is feasible.

Longlines can potentially impact stocks of tilefish. The population estimate of tilefish in the study area (39–128) and the catch made by the intensive fishing effort (79) indicate that from 62 to 100% of the fish were taken out of the area by an effort of approximately 6000 hook-hours, which is a 1.5–2 day effort by a commercial longliner (Prytherch 1983). Catch rates in the northern Gulf of Mexico in 1982 averaged 1–6 fish per 100 hook-hours (Prytherch 1983). Based on the estimated population size within the area, the initial catch rates indicate that the longline effectively catches all fish out of an area that is at least 12 m wide. Some fish are attracted from greater distances (Grimes et al. 1982), and some near the longline are not caught. But the number removed from the population is equal to the length of the longline × a width of 12 m × fish density.

Estimates of the total portion of the Gulf of Mexico inhabited by tilefish have not been developed, but the optimal areas are limited by depth, temperature, and bottom type (Grimes et al. 1980, 1986; Grossman et al. 1985). This, combined with slow growth rate, longevity, and low natural mortality (Turner et al. 1983, Harris and Grossman 1985), indicate that overfishing could easily take place if substantial effort is expended in tilefish habitat. This is especially true in light of the susceptibility to mass mortalities caused by sudden temperature reductions (Hachey 1955). Data from South Carolina tilefish habitat show a substantial decline in catch rate and mean size over a 4–5 year period with low to moderate effort (Low et al. 1983). Further, the number of tilefish burrows per km^2 in the Middle and South Atlantic Bights in the early 1980s was 241 and 125, respectively (Able et al. 1987). These estimates are much lower than the 1600 burrows per km^2 in the Gulf of Mexico estimated in this study.

More extensive longline studies of yellowedge grouper catches are required to assess the effect of longlines on these populations. The population estimate of yellowedge grouper in the yellowedge study site from fishing activities was not significant, but the best estimate (26 animals) from the non-significant regression may be realistic. The regression indicated that similar fractions of the yellowedge grouper population (40%) would be caught at similar levels of effort as compared with tilefish, and similar impacts from the longline fishery might be expected. However, the results may not be analagous because different gear were used in the two areas.

While the association with hard substrate and high relief was expected for yellowedge and other groupers, the burrowing habits were not expected. A detailed description of grouper habitat and burrow characteristics have been provided by Jones et al. (1989). The finding that this species also inhabits burrows was especially significant. If this were the only habitat, it would limit their distribution and increase their susceptibility to fishing once they are located. However, this species is also associated with rock and reef habitat typical of other grouper species. This diversity of habitat should enhance the survivability of the species overall, but it makes a part of the population more susceptible to longline fishing.

The uneven distribution of tilefish and yellowedge grouper between fished and unfished areas was also unexpected. Reasons for the differential distribution are not apparent. But the effects of depth, temperature, and bottom type on the fish were probably involved.

This study demonstrates the need for additional research to estimate population sizes and life-history parameters for deepwater Gulf fishes to quantify the amount of fishing they can support. Routine monitoring of these populations could be accomplished with longlines fished during August through October. Limited data on tilefish and yellowedge grouper have been collected with bottom longlines by the National Marine Fisheries Service since 1968 (Table 4). However, the data are insufficient to identify trends.

Table 4

Mean catch (no./100 hook-hours) ± 95% confidence interval of tilefish and yellowedge grouper on NMFS bottom longline sets each month, 1968–84, in the area bounded by 27°37′–27°50′ lat. and 93°32′–95°21′ long. Numbers in parentheses indicate numbers of sets. Blanks indicate no data collected.

Species	Year	Jan.	Feb.	May	Aug.	Sep.	Oct.	Nov.
Tilefish	1968	9.5 ± 12.2 (8)						
	1973			20.8 ± 6.9			6.8 ± 5.2 (14)	
	1975							2.1 ± 6.2 (3)
	1976				7.1 ± 4.1 (8)			
	1977		9.1 ± 9.3 (6)		10.0 ± 12.9 (4)			
	1983				6.1 ± 3.4 (7)			
	1984			6.9 ± 8.0 (9)		3.1 ± 1.3 (57)		
Yellowedge grouper	1968	5.5 ± 8.3 (11)						
	1973			18.4 (1)			0.7 ± 1.2 (8)	
	1975							0.0 (1)
	1976				2.5 ± 6.0 (3)			
	1977		0.0 ± 0.0 (3)					
	1981					0.0 ± 0.0 (2)		
	1983				3.7 ± 6.7 (8)			
	1984			1.2 ± 2.1 (6)		2.1 ± 1.3 (16)		

Natural and fishing mortality estimates, growth rates, population structure, distribution throughout all life stages, and weight landed should be determined and used in population simulation models to assist managers in protecting these resources from overfishing. A fishery-independent sampling program using longlines is recommended for monitoring the status of tilefish, hake, barrelfish, longspine scorpionfish, Cuban dogfish, and possibly yellowedge grouper populations. This is a more appropriate source of fish for mortality estimates than are commercial landings (Low et al. 1983, Winters and Wheeler 1985) and can yield reliable population size estimates if catchability coefficients are known.

Acknowledgments

Funding for submersible activities involved in this project was provided by the NOAA Office of Undersea Research. The Harbor Branch Oceanographic Institute participated on a cost-sharing basis. Support for the fishing activities and the NOAA Ship *Oregon II* was provided by the National Marine Fisheries Service. We would like to thank Captain Bill Abney and the crew of the RV *Johnson* for their dedication and long hours, and submersible pilots Tim Askew, Marshall Flake, Don Liberatore, Steve Hall, and the submersible support crew for the *Johnson-Sea-Link* for doing whatever was necessary to accomplish mission objectives. We would also like to thank Captain Gunnar Gudmundsson and the crew of the NOAA Ship *Oregon II* for their support and, especially, G. Michael Russell for serving as field party chief to insure accomplishment of planned fishing activities. Thanks are also extended to Art Crowe and Maury Osborn of the Texas Parks and Wildlife Department for their help in baiting hooks and collecting data. Suggestions from two anonymous reviewers were very helpful in improving the content of the manuscript.

Citations

Able, K.W., C.B. Grimes, R.A. Cooper, and J.R. Uzmann
1982 Burrow construction and behavior of tilefish, *Lopholatilus chamaeleonticeps* in Hudson Submarine Canyon. Environ. Biol. Fishes 7:199–205.

Able, K.W., D.C. Twichell, C.B. Grimes, and R.S. Jones
1987 Sidescan Sonar as a tool for detection of demersal fish habitats. Fish. Bull., U.S. 85:725–736.

Braaten, D.O.
1969 Robustness of the DeLury population estimator. J. Fish. Res. Board Can. 26:339–355.

Cochran, W.G.
1977 Sampling techniques. John Wiley, NY, 428 p.

Cody, T.J., B.E. Fuls, G.C. Matlock, and C.E. Bryan
1981 Assessment of bottom longline fishing off the central Texas coast, a completion report. Tex. Parks Wildl. Dep., Coast. Fish. Branch, Manage. Data Ser. 22, Austin, 51 p.

Freeman, B.L., and S.C. Turner
1977 Biological and fisheries data on tilefish, *Lopholatilus chamaeleonticeps*, Goode and Bean. Tech. Rep. 5, Sandy Hook Lab., Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732, 41 p.

Goodman, L.A.
1960 On the exact variance of products. J. Am. Stat. Assoc. 55:708–713.

Graham, G.
1978 Preliminary progress report: Bottom longline investigations. Unpubl. manuscr., Sea Grant Coll. Prog., Tex. A&M Univ., College Station, 30 p.

Grimes, C.B., K.W. Able, and S.C. Turner
1980 A preliminary analysis of the tilefish, *Lopholatilus chamaeleonticeps*, fishery in the Mid-Atlantic Bight. Mar. Fish. Rev. 42(11):13–18.
1982 Direct observation from a submersible vessel of commercial longlines for tilefish. Trans. Am. Fish. Soc. 111:94–98.

Grimes, C.B., S.C. Turner, and K.W. Able
1983 A technique for tagging deepwater fish. Fish. Bull., U.S. 81:663–666.

Grimes, C.B., K.W. Able, and R.S. Jones
1986 Tilefish *Lopholatilus chamaeleonticeps*, habitat, behavior, and community structure in Mid-Atlantic and southern New England waters. Environ. Biol. Fishes 15(4):273–292.

Grossman, G.D., M.J. Harris, and J.E. Hightower
1985 The relationship between tilefish, *Lopholatilus chamaeleonticeps*, abundance and sediment composition off Georgia. Fish. Bull., U.S. 83:443–447.

Hachey, H.B.
1955 Water replacements and their significance to fishery. Pap. Mar. Biol. Oceanogr., Deep-Sea Res. Suppl. to Vol. 3, p. 68–73.

Harris, M.J., and G.D. Grossman
1985 Growth, mortality, and age composition of a lightly exploited tilefish substock off Georgia. Trans. Am. Fish. Soc. 114:837–847.

Jones, R.S., E.J. Gutherz, W.R. Nelson, and G.C. Matlock
1989 Burrow utilization by yellowedge grouper, *Epinephelus flavolimbatus*, in the northwestern Gulf of Mexoci. Environ. Biol. Fishes 26:277–284.

Katz, S.J., C.B. Grimes, and K.W. Able
1983 Delineation of tilefish, *Lopholatilus chamaeleonticeps*, stocks along the United States east coast and in the Gulf of Mexico. Fish. Bull., U.S. 81:41–50.

Low, R.A., G.F. Ulrich, and F. Blum
1983 Tilefish off South Carolina and Georgia. Mar. Fish. Rev. 45(4-6):16–26.

Nelson, W.R., and J.S. Carpenter
1968 Bottom longline explorations in the Gulf of Mexico. Commer. Fish. Rev. 30(10):57–62.

Pennington, M.
1983 Efficient estimators of abundance, for fish and plankton surveys. Biometrics 39:281–286.
1986 Some statistical techniques for estimating abundance indices from trawl surveys. Fish. Bull., U.S. 84:519–525.

Prytherch, H.F.
1983 A descriptive survey of the bottom longline fishery in the Gulf of Mexico. NOAA Tech. Memo. NMFS-SEFC-122, Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Miami, FL 33149, 33 p.

Ricker, W.E.
1975 Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191, 382 p.

Robins, C.R., R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea, and W.B. Scott
1980 A list of common and scientific names of fishes from the United States and Canada. Spec. Publ. 12, Am. Fish. Soc., Bethesda, MD, 174 p.

SAS Institute, Inc.
1982 SAS user's guide: Statistics, version 5 edition. SAS Inst., Inc., Cary, NC, 965 p.

Sokal, R.R., and F.J. Rohlf
1981 Biometry, 2d ed. W.H. Freeman, San Francisco, 776 p.

Turner, S.C.
1986 Population dynamics of and the impact of fishing on tilefish, *Lopholatilus chamaeleonticeps*, in the Middle Atlantic–Southern New England region during the 1970's and early 1980's. Ph.D. diss., Rutgers Univ., New Brunswick, NJ, 289 p.

Turner, S.C., C.B. Grimes, and K.W. Able
1983 Growth, mortality, and age/size structure of the fisheries for tilefish, *Lopholatilus chamaeleonticeps*, in the Middle Atlantic–Southern New England region. Fish. Bull., U.S. 81:751–763.

Twichell, D.C., C.B. Grimes, R.S. Jones, and K.W. Able
1985 The role of erosion by fish in shaping topography around Hudson Submarine Canyon. J. Sediment. Petrol. 55:712–719.

White, G.C., D.R. Anderson, K.P. Burnham, and D.L. Otis
1982 Capture-recapture and removal methods for sampling closed populations. LA-8787-NERP, Los Alamos Natl. Lab., Los Alamos, NM, 235 p.

Winters, G.H., and J.P. Wheeler
1985 Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. 42:989–998.

Wolf, R.S., and W.F. Rathjen
1974 Exploratory fishing activities of the UNDP/FAO Caribbean Fishery Development Project, 1965–1971: A summary. Mar. Fish. Rev. 36(9):1–8.

Abstract.—Collections were made for gulf butterfish *Peprilus burti* along a cross-shelf transect at depths of 5–100 m in the Gulf of Mexico off Texas from October 1977 to July 1980. Butterfish mature at 100–160 mm fork length as they approach age I. Spawning occurs primarily from September through May, but length frequencies indicate it concentrates, or is most successful, in distinct "Winter" (late January–mid-May) and "Fall" (early September–late October) periods that coincide with downcoast, alongshore currents (toward Mexico). Gonad data and persistence of small fish indicate spawning in winter, but at a low level. Spawning probably occurs offshore and upcoast toward the northcentral Gulf. Surface currents of the cyclonic shelf gyre probably transport eggs/larvae inshore and downcoast to recruit to the bottom in water 5–27 m deep, used as nurseries by butterfish when they are 2–5 months old. Butterfish disperse offshore as they mature and congregate in 36–100 m depths when they are 9–12 months old. They average 130–146 mm in fork length at age I in the northwestern Gulf, but 120–124 mm at age I and about 170 mm at age II in the northcentral Gulf. Estimates for the von Bertalanffy growth parameters L_∞, K, and t_0 were 164 mm, 1.99/year, and −0.20 years, respectively, for pooled northwestern Gulf Winter cohorts and 141 mm, 2.69/year, and −0.06 years, respectively, for pooled Fall cohorts. Somatic growth ceases as spawning approaches in the northwestern Gulf, but fish from the northcentral Gulf show large annual size increments. Butterfish reach about 200 mm in fork length, the largest ones occurring in the northcentral Gulf. Apparent maximum ages are 1–1.5 years in the northwestern Gulf, and 2–2.5 years in the northcentral Gulf. Differences in population attributes suggest complete mortality at age I in the northwestern Gulf or some unknown combination of an offshore and permanent contranatant spawning or postspawning emigration of adults to the northcentral Gulf. The genus *Peprilus* shows zoogeographic differences in population dynamics near Cape Hatteras, North Carolina.

Manuscript accepted 1 October 1990.
Fishery Bulletin, U.S. 89:101–116 (1991).

Reproduction, Age and Growth, and Movements of the Gulf Butterfish *Peprilus burti**

Michael D. Murphy

Florida Marine Research Institute, Florida Department of Natural Resources
100 Eighth Avenue SE, St. Petersburg, Florida 33701

Mark E. Chittenden Jr.

Department of Wildlife and Fisheries Sciences, Texas A&M University
College Station, Texas 77843
Present address: Virginia Institute of Marine Science, School of Marine Science
College of William and Mary, Gloucester Point, Virginia 23062

The gulf butterfish *Peprilus burti* ranges in the Gulf of Mexico (Gulf) from the Yucatan Peninsula to Tampa Bay, Florida (Horn 1970) and may occur along the U.S. southeast Atlantic coast, depending upon its systematic status and range extensions during cold spells (Caldwell 1961, Collette 1963, Horn 1970, Perschbacher et al. 1979). This abundant species is important in the industrial fishery and is commonly discarded by the shrimp fishery in the northern Gulf (Roithmayr 1965, Franks et al. 1972, Gutherz et al. 1975, Chittenden and McEachran 1976). Recent exploratory surveys have found large, commercially valuable concentrations of *P. burti* in the northern Gulf (Vecchione 1987). A preliminary biomass estimate for this area is 177,000 MT per 10,164 square miles (Gledhill unpubl.).

The life history and population dynamics of this species have not been described in detail, only as brief notes in numerous faunal studies including Gunter (1945), Hildebrand (1954), Miller (1965), Franks et al. (1972), Christmas and Waller (1973), Chittenden and McEachran (1976), and Allen et al. (1986). The paucity of information reflects difficulty in age determination. Allen et al. (1986) found that hard parts such as otoliths, scales, opercula, and vertebrae were not useful in age determination.

In this paper we use an extensive set of length frequencies to infer age of *P. burti* and to describe size and age at maturity, spawning seasonality and areas, recruitment, seasonal distribution and movements, growth, maximum size and age, and weight-length, girth-length, and total, fork, and standard length relationships. We also discuss hydrographic conditions associated with spawning areas and recruitment, and zoogeographic differences in population dynamics in *Peprilus* near Cape Hatteras, North Carolina.

Methods

Collections for *Peprilus burti* were made along a cross-shelf transect in the Gulf off Freeport, Texas (Fig. 1) from October 1977 through July 1980 aboard a chartered shrimp trawler using twin 10.4-m (34-ft) shrimp trawls with a tickler chain and 4.4-cm stretched mesh in the cod end. Initial stations were located at depths of 9, 13, 16, 18, 22, 27, 36, and 47 m. Sampling was expanded to include stations at 5 and 24 m after November 1978 and at 55, 64, 73, 82,

*Contribution No. 1625 of the Virginia Institute of Marine Science, College of William and Mary.

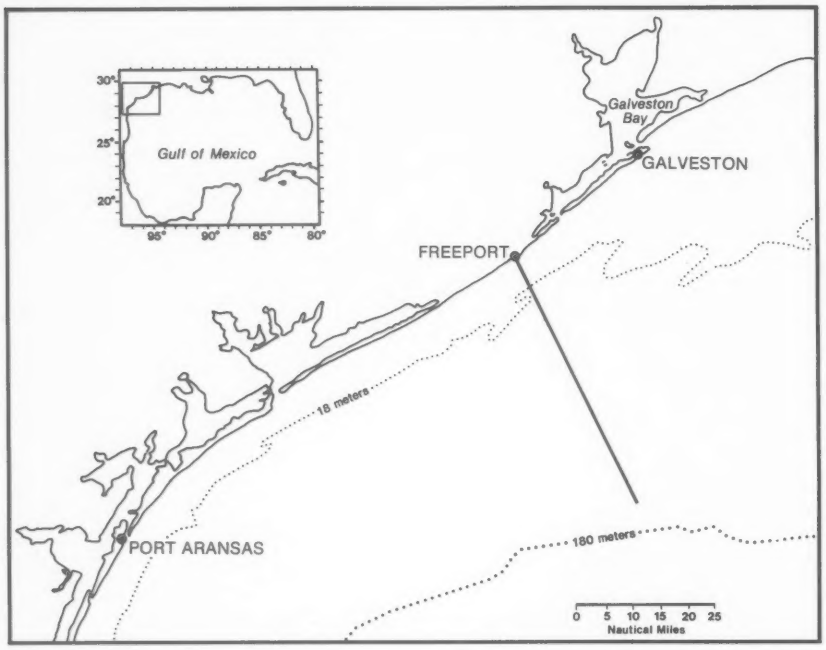


Figure 1
Location of sampling area off Freeport, Texas.

and 100 m after May 1979. Collections were made during the day through September 1978; thereafter, a day and a night cruise usually were made each month. Usually two tows, consisting of 10 minutes of bottom time, were made at each depth. Exceptions were 8 tows made at 16 m, and 24 tows made at 22 m, and only one tow made at most depths prior to October 1978. Our spatial sampling design was a single cross-shelf transect from a sampling frame that encompassed much of the northern Gulf.

All *P. burti* were culled from the catch, measured for total length (TL), fixed in 10% formalin for 2–4 days, and then stored in 70% ethanol. For the period December 1978–November 1979 a total of 300 fish, if available, was selected each month after stratifying the catch into cohorts determined by length-frequency analysis (see below). Specimens were then randomly selected within strata to determine total length, fork length (FL), standard length (SL), total weight (TW), gonad weight (GW), and girth (G) measured vertically from the dorsal fin to the preanal pterygiophore. Sagittal otoliths were removed from individuals larger than 75 mm, teased free of saccular and labyrinthian tissue, and then stored dry for later immersion in water and viewing with reflected light under a dissecting microscope. Female and immature fish were assigned gonad maturity stages (Table 1) modified from Kesteven's system (Bagenal and Braum 1971). Gonad weight and

Table 1
Description of gonad maturity stages assigned to immature and female *P. burti*.

Stage	Description
1 Immature	Gonads barely or not visible; sex indistinguishable to naked eye.
2 Maturing Virgin	Gonads small, opaque; usually thin, streamer-like, running along posterioventral wall of body cavity; sex indistinguishable to naked eye.
3 Early Developing/ Resting	Sex distinguishable; individual eggs not visible to naked eye but ovarian lamellae visible; ovaries occupy <20% of body cavity.
4 Late Developing I	Ovaries occupy 20–50% of body cavity; individual eggs visible in close examination; eggs opaque.
5 Late Developing II	Ovaries occupy 50–80% of body cavity; individual eggs distinguishable; eggs opaque.
6 Gravid	Ovaries occupy >50% of body cavity; translucent eggs present, but make up <50%.
7 Ripe	Ovaries occupy >50% of body cavity; >50% of eggs translucent.
8 Spawning/Spent	Ovaries flaccid, pink, with few eggs present; fish large enough to have spawned.

Table 2

Final quadratic growth regressions, calculated hatching dates, and von Bertalanffy equations for individual *Peprilus burti* cohorts and pooled Fall and Winter cohorts. Fits regress mean observed fork lengths (mm FL) on age in days (Days) for the quadratic and on age in years (Years) for the von Bertalanffy growth equations. All regressions are significant at $\alpha = 0.05$.

Cohort	Final quadratic growth equation	r^2	Final calculated hatching date	von Bertalanffy growth equation
$Fall_{77}$	$FL = 0.09 + 0.6004(Days) - 0.0007(Days)^2$	0.93	25 Sep 77	$FL = 139(1 - \exp(-2.22(Years + 0.050)))$
$Fall_{78}$	$FL = -0.14 + 0.6971(Days) - 0.0009(Days)^2$	0.87	8 Sep 78	$FL = 138(1 - \exp(-3.81(Years + 0.122)))$
$Fall_{79}$	$FL = -0.16 + 0.7234(Days) - 0.0010(Days)^2$	0.97	15 Sep 79	Data not adequate to fit alone
Fall pooled	$FL = 4.04 + 0.6386(Days) - 0.0008(Days)^2$	0.91	— — —	$FL = 141(1 - \exp(-2.69(Years + 0.063)))$
$Winter_{78}$	$FL = -0.10 + 0.1741(Days) - 0.0011(Days)^2$	0.95	30 Jan 78	$FL = 133(1 - \exp(-3.06(Years + 0.055)))$
$Winter_{79}$	$FL = 0.14 + 0.6931(Days) - 0.0008(Days)^2$	0.94	16 Mar 79	$FL = 170(1 - \exp(-1.98(Years + 0.043)))$
$Winter_{80}$	$FL = -0.09 + 0.6975(Days)$	0.93	22 Mar 80	Data not adequate to fit alone
Winter pooled	$FL = 8.18 + 0.6327(Days) - 0.0007(Days)^2$	0.93	— — —	$FL = 164(1 - \exp(-1.99(Years + 0.200)))$
Fall and Winter pooled	$FL = 6.28 + 0.6362(Days) - 0.0008(Days)^2$	0.91	— — —	

stage were also determined for randomly selected fish in October 1978 and during December 1979–February 1980 to verify spawning seasons. All lengths presented are fork lengths, and all length frequencies are moving averages of three, unless specified otherwise.

We also made collections in the northcentral Gulf, at depths of 9–91 m, aboard the FRS *Oregon II* east (89°00′W–89°30′W) and west (89°30′W–91°30′W) of the Mississippi River during 10–19 April 1980 and 21 April–1 May 1980, respectively (Rohr et al. 1980). Fish were sampled from these catches without randomization and measured (FL) to compare with size and age compositions in the northwestern Gulf.

Age was determined by length-frequency analysis, that is, the modal group progression analysis modification (Jearld 1983) of the Petersen method (Lagler 1956, Tesch 1971). Cohorts were specified by the season and year when they hatched, for example, $Fall_{79}$. Cohorts hatched during the periods January–May and September–October are hereafter referred to as Winter and Fall cohorts, respectively; this abbreviated terminology corresponds with the major spawning each period (see "Maturation and Spawning Periodicity"). Arithmetic means were used to describe central tendencies in cohort length frequencies.

Mean hatching dates used to approximate time scales to calculate growth were determined by a one-step iterative process following Standard and Chittenden (1984). A hatching date of 1 March was assigned to start iterations for the $Winter_{79}$ and $Winter_{80}$ cohorts because, in those groups, fish 30–75 mm, assumed to be 2–4 months old, first appeared mid-May to mid-June. A hatching date of 1 February was assigned to start iterations for the $Winter_{78}$ cohort because, in that group, fish 20–50 mm, assumed to be 1–3 months old, became abundant in mid-April. A hatching date of 1 September was assigned to start the approximation for Fall cohorts because fish 30–75 mm, assumed to be 2–4 months old, first appeared November through early December. Quadratic regression of length-on-age in days was then used to estimate initial x-intercepts for each cohort. Final hatching dates were calculated by using x-intercepts to readjust the initial x-variable (time) scale, so that each final quadratic growth curve passed through the origin (Table 2). Descriptions of spawning periodicity using length frequencies assume early size and age combinations (see Results) predicted from quadratic regression of length-on-age pooling all Winter and Fall cohorts (Table 2). Von Bertalanffy growth equations were fit to length and age (in years) data using the nonlinear least-square parameter estimation procedure in FSAS (Saila et al. 1988). Data points described a curvilinear regression and evidenced an asymptote, so equations presented met the minimum requirements for a von Bertalanffy fit (Knight 1968, Gallucci and Quinn 1979).

Maximum age was approximated by the Beverton–Holt model parameter t_L (Gulland 1969) following the definition that only 0.5–1.0% of the catch exceeds age t_L or its corresponding length (Alverson and Carney 1975, DeVries and Chittenden 1982). Maximum sizes and ages, and sizes-at-age, presented are termed apparent, because they may be affected by emigration of fish approaching age I; if so, they underestimate maximum size and age, and sizes-at-age.

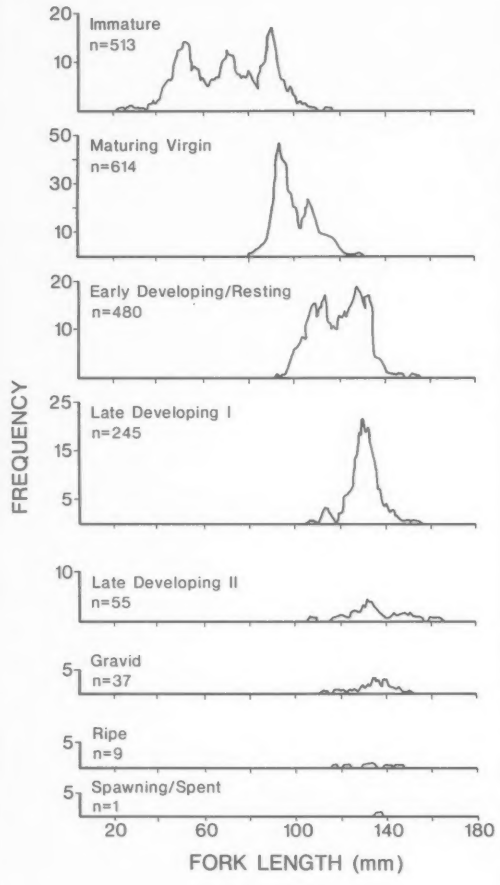


Figure 2
Length frequencies of immature and female *Peprilus burti* by maturity stage (see Table 1).

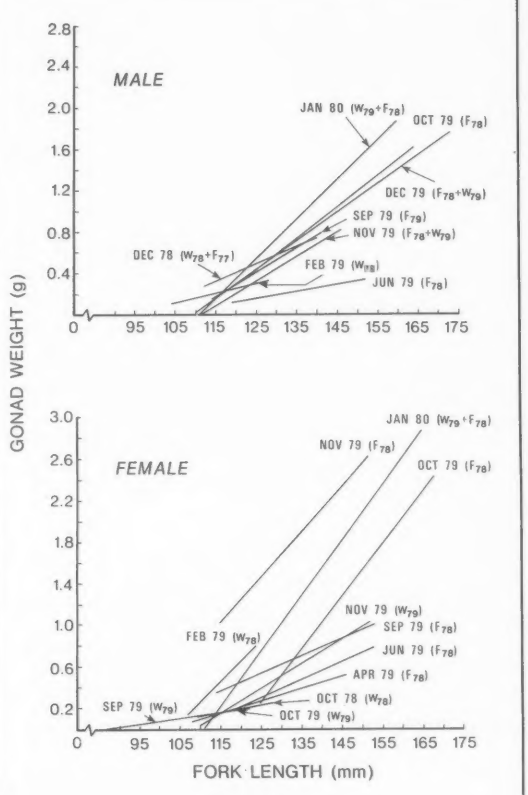


Figure 3
Monthly gonad weight–length regressions for *Peprilus burti* by cohort group (W = Winter, F = Fall). Line lengths show observed size ranges.

Figure 4
(facing page and overleaf)
Monthly length frequencies of *Peprilus burti* off Freeport, Texas.

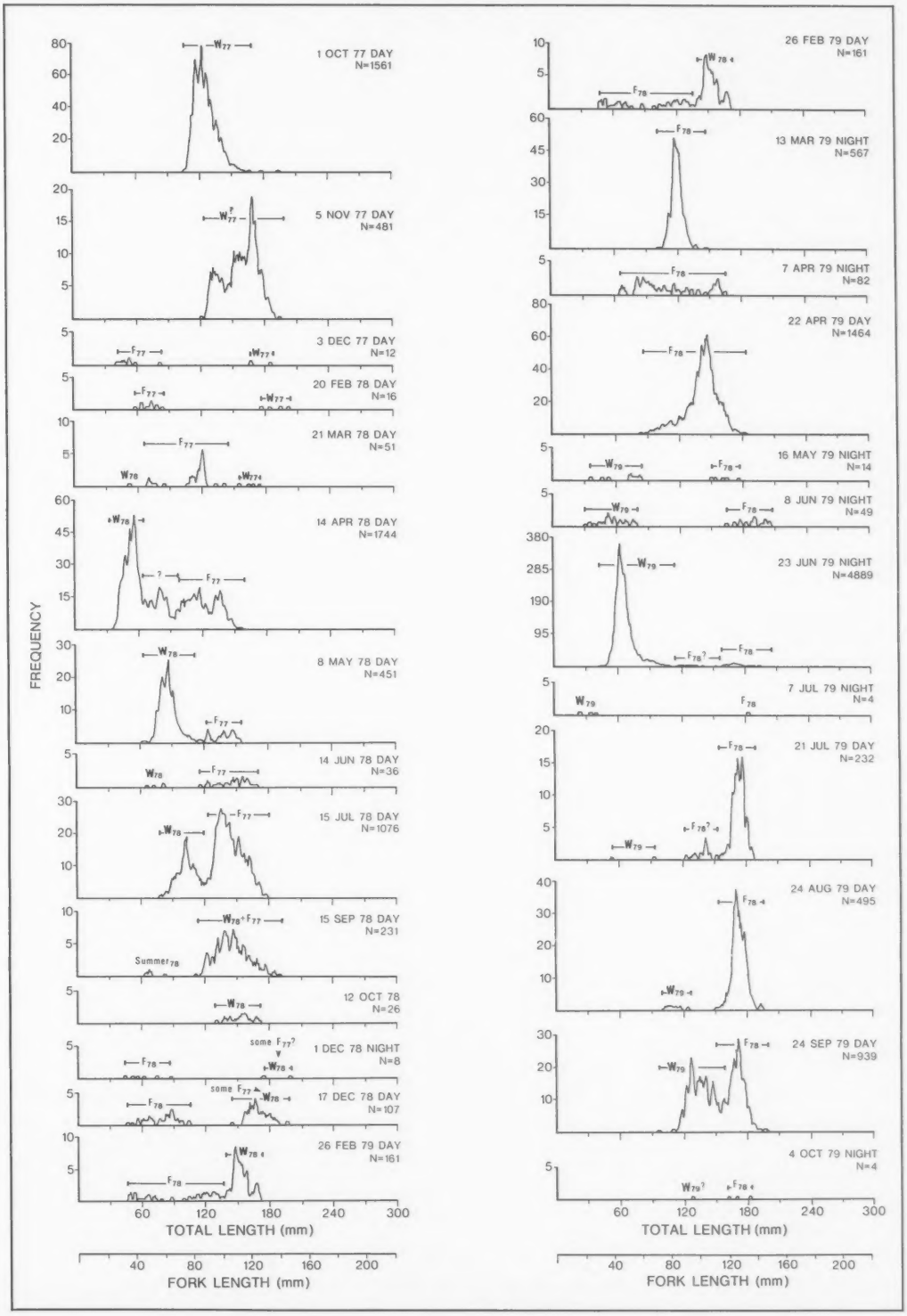
Results

Maturation and spawning periodicity

Peprilus burti mature at 100–160 mm in length. Few fish larger than 100 mm were immature (Fig. 2). Males were identifiable at 100–110 mm when the testes became creamy white, but they were difficult to stage macroscopically. Females were 95–155 mm and 105–165 mm in Early Developing and Late Developing stages, respectively. Most Gravid and Ripe females were 120–150 mm, the smallest being 113 mm. These sizes-at-maturity are supported by regressions of gonad weight on fork length (Fig. 3) in which x-intercepts for both sexes usually were 95–110 mm during September through February, a period that brackets much of the broad spawning period when fish should be maturing. Age compositions and sizes-at-age presented later indicate *P. burti* mature to first spawn at 9–16 months.

Peprilus burti spawn primarily during the broad period of September through May. Fish 30–40 mm, which occurred mid-November to early July (Fig. 4), were 1.5 months of age April–July and mid-November–December based on quadratic regressions of size-on-age for pooled Winter and Fall cohorts (Table 2).

Little spawning of *P. burti* occurs June through August. Fish 30–40 mm, 1.5 months-old, were not captured late July to early November (Fig. 4). No distinct,


FREQUENCY
1 OCT 77 DAY N=1561
5 NOV 77 DAY N=481
3 DEC 77 DAY N=12
20 FEB 78 DAY N=16
21 MAR 78 DAY N=51
14 APR 78 DAY N=1744
8 MAY 78 DAY N=451
14 JUN 78 DAY N=36
15 JUL 78 DAY N=1076
15 SEP 78 DAY N=231
12 OCT 78 N=26
1 DEC 78 NIGHT N=8
17 DEC 78 DAY N=107
26 FEB 79 DAY N=161
13 MAR 79 NIGHT N=567
7 APR 79 NIGHT N=82
22 APR 79 DAY N=1464
16 MAY 79 NIGHT N=14
8 JUN 79 NIGHT N=49
23 JUN 79 NIGHT N=4889
7 JUL 79 NIGHT N=4
21 JUL 79 DAY N=232
24 AUG 79 DAY N=495
24 SEP 79 DAY N=939
4 OCT 79 NIGHT N=4
TOTAL LENGTH (mm)
FORK LENGTH (mm)

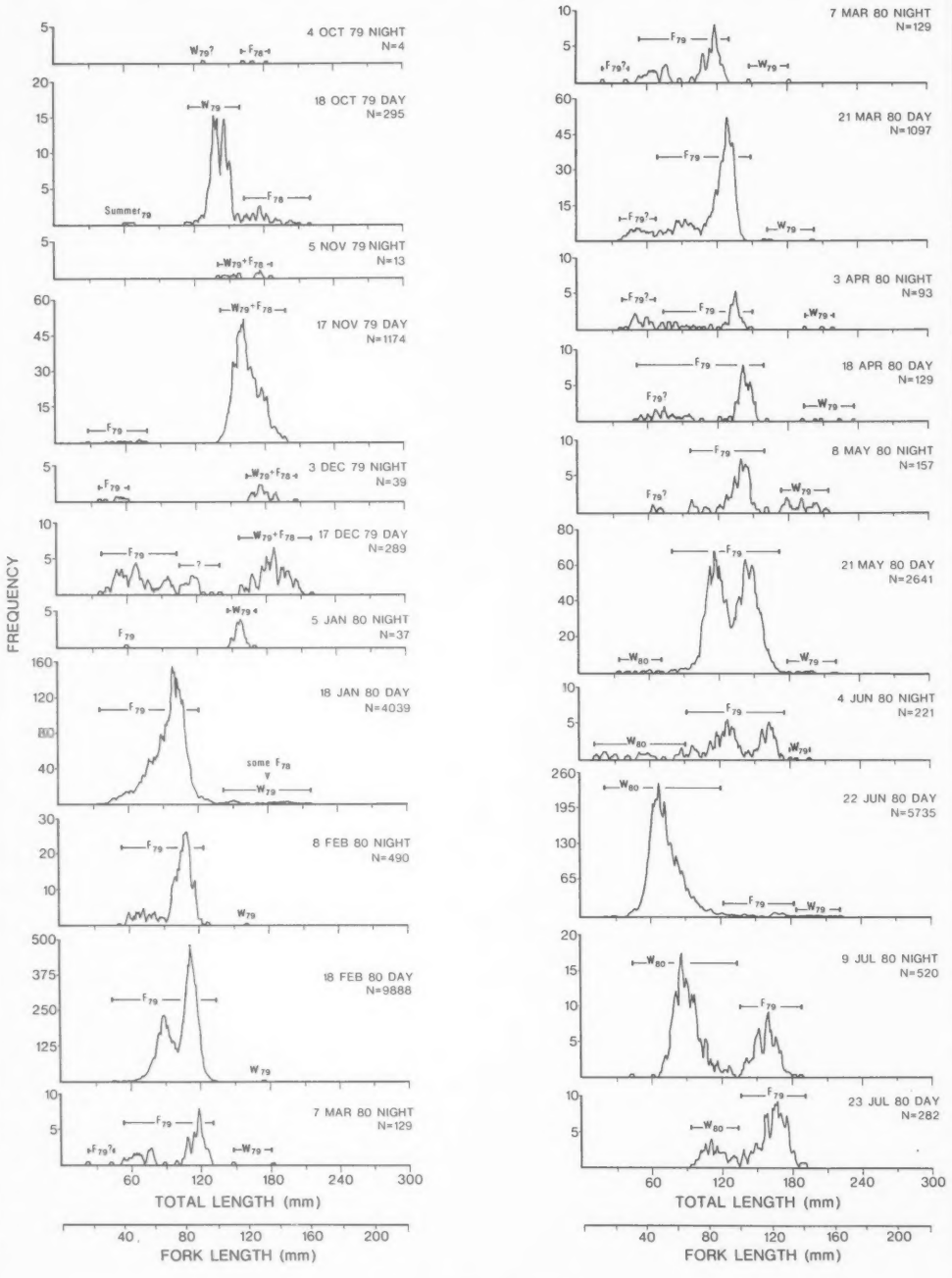

4 OCT 79 NIGHT N=4
18 OCT 79 DAY N=295
5 NOV 79 NIGHT N=13
17 NOV 79 DAY N=1174
3 DEC 79 NIGHT N=39
17 DEC 79 DAY N=289
5 JAN 80 NIGHT N=37
18 JAN 80 DAY N=4039
8 FEB 80 NIGHT N=490
18 FEB 80 DAY N=9888
7 MAR 80 NIGHT N=129
21 MAR 80 DAY N=1097
3 APR 80 NIGHT N=93
18 APR 80 DAY N=129
8 MAY 80 NIGHT N=157
21 MAY 80 DAY N=2641
4 JUN 80 NIGHT N=221
22 JUN 80 DAY N=5735
9 JUL 80 NIGHT N=520
23 JUL 80 DAY N=282
FREQUENCY
TOTAL LENGTH (mm)
FORK LENGTH (mm)

Figure 4 (continued)

abundant groups of fish 30–60 mm originated then, and the smallest fish caught then usually reflected the more slowly growing Winter-spawned individuals. The few fish 50–60 mm, about 2.5–3 months of age on average, caught September to mid-November, and the one Gravid fish captured in July, probably indicate some summer spawning (Fig. 5).

Peprilus burti spawn primarily during discrete Winter (late January–mid-May) and Fall (early September–late October) periods. Length compositions were consistently bimodal off Texas, and modal groups originated from Winter and Fall spawning periods (Fig. 4). Winter-spawned fish first appeared mid-April to early July at lengths of 30–75 mm at an average age of 1.5–4.5 months, which indicates spawning from about late January to mid-May. Fall-spawned fish first appeared mid-November to early December at lengths of 30–75 mm and an average age of 1.5–4.5 months, which indicates spawning from about early September to late October. Modes for Winter cohorts are readily followed in the periods: (1) mid-April 1978–late February 1979, (2) mid-May 1979–mid-June 1980, and (3) late May–late July 1980. Modes for Fall cohorts can be followed in the periods: (1) early December 1977–mid-July 1978, (2) December 1978–mid-October 1979, and (3) mid-November 1979–late July 1980. Calculated mean hatching dates occurred during late January to March for Winter groups and during September for Fall groups (Table 2).

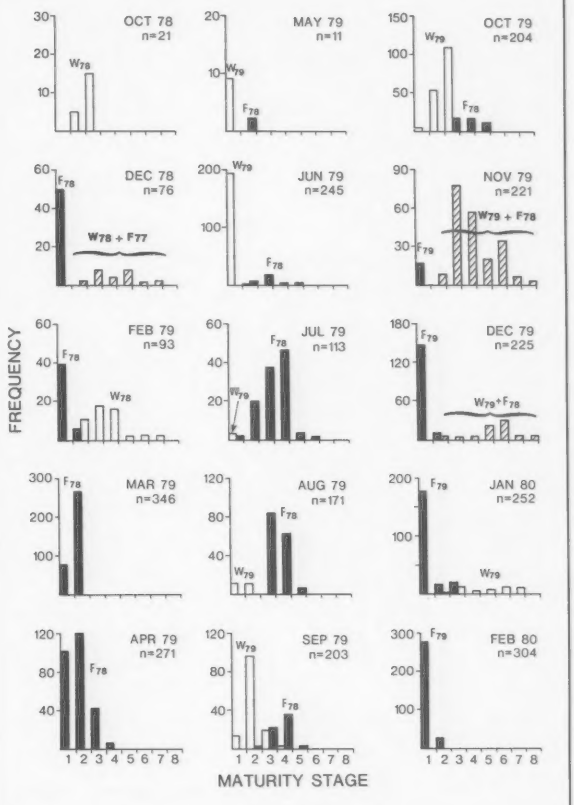


Figure 5

Monthly maturity stages (Table 1) of immature and female *Peprilus burti*. Bars indicate Fall (F, dark) and Winter (W, light) cohorts and mixtures of two cohorts (diagonals) in which cohort identity is not clear for individual fish.

In contrast to length frequencies, gonad weight and maturity data indicate *P. burti* spawns during much of the fall and winter. Gonad weight regressions had maximum slopes and elevations and usually were significant September through February (Fig. 3). Regressions had lower slopes and elevations and usually were not significant March through August (Murphy 1981, Table 2). Most Gravid and/or Ripe fish were captured November through February (Fig. 5).

The end of the Fall spawning period is not clear, but length frequencies suggest low-level spawning, or spawning success, during late fall and early winter. The consistently bimodal length frequencies must reflect some temporal separation in spawning that originates then. $Fall_{79}$ fish recruited in abundance by mid-January to mid-February 1980 when they were 60–105 mm long and 3–7 months of age (Fig. 4). $Fall_{78}$ fish recruited in abundance by mid-March 1979 when they were 90–110 mm and 5.5–7.5 months of age. These data suggest peak fall spawning ends by about late October. No abundant, distinct groups of fish 30–60 mm and 1.5–3 months of age originated during any late-fall or early-winter period studied (Fig. 4), although 30–75 mm fish—which we labeled Fall-spawned fish—persisted January through May in 1979 and 1980 and probably reflect some winter spawning.

Cohort spawning and recruitment periodicity vary within and between years. $Winter_{78}$ fish appeared as an abundant, distinct group in mid-April, but few recruited thereafter (Fig. 4). In contrast, $Winter_{79}$ and $_{80}$ fish did not form abundant, distinct groups until June, although a few fish appeared in May. Fall groups first appeared mid-November to early December. However, the bimodal size frequencies of the $Fall_{79}$ cohort in the period mid-February to early June 1980 suggest intragroup variation in spawning or recruitment success and periodicity similar to that for winter cohorts. We have interpreted the lower mode

of the $Fall_{79}$ cohort as actually being part of that cohort; the lower mode first became distinct in February 1980 when those fish were primarily 55–75 mm long and about 4 months of age, which would suggest early October to early November hatching.

Recruitment, movements, and nurseries

Fall cohorts of *P. burti* seemingly recruit in abundance at an older age (4–5 months) than Winter fish (2–4 months) off Texas. Winter fish formed abundant, distinct groups soon after first appearing mid-April to early June at 30–75 mm in length when 1.5–4.5 months old (Fig. 4). Fall fish did not form abundant, distinct groups until winter to early spring, although they first appeared mid-November to early December when 30–75 mm and 1.5–4.5 months old.

Young *P. burti* recruit to the bottom off Texas primarily in 5–27 m depths when 2–5 months old. $Winter_{79}$ fish 2–4 months old and 35–70 mm were captured only at 22 m in May 1979 (Figs. 4, 6). They occurred from 16–55 m during the period June through August 1979 (primarily June) but were most abundant at 22–27 m; few were shallower than 22 m or deeper than 36 m. Recently hatched $Fall_{79}$ fish 25–70 mm long were captured only at 5–9 m in mid-November 1979 (Figs. 4, 6). $Fall_{79}$ fish occurred only at 5–27 m (primarily 22–27 m) December 1979 through February 1980 when 3–5 months old. Similarly, $Fall_{78}$ fish were abundant at 5–27 m March through May when 7–9 months old, but few occurred in deeper water.

Juvenile *P. burti* disperse offshore as they mature and approach age I. $Winter_{79}$ fish were most abundant at 13–27 m depths September through November 1979 when 6–8 months old (Fig. 6). However, none occurred shallower than 22 m December 1979 through February 1980, when they were 9–11 months old; most were at 36–100 m. The largest $Fall_{79}$ individuals occurred in the deepest water December 1979 through February 1980, the size gradient suggesting gradual movement offshore. $Fall_{78}$ fish were almost exclusively at 5–27 m from March through May 1979 when 7–9 months old, but they were at 36–100 m from June through August when 10–12 months old.

Age determination using otoliths

Whole otoliths of *P. burti* apparently cannot be readily aged. Only 984 of 2461 whole otoliths examined had apparent internal features. Many were entirely opaque or lacked a distinct boundary between opaque and hyaline zones, possibly due to initial preservation or storage fluids, though fresh otoliths showed similar features. Only 11 of the 984 legible otoliths had an apparent annulus. These 11 fish were 120–160 mm in length and could have been about age I by length-frequency analysis. Annuli frequently were not apparent for fish that were age I by length frequencies.

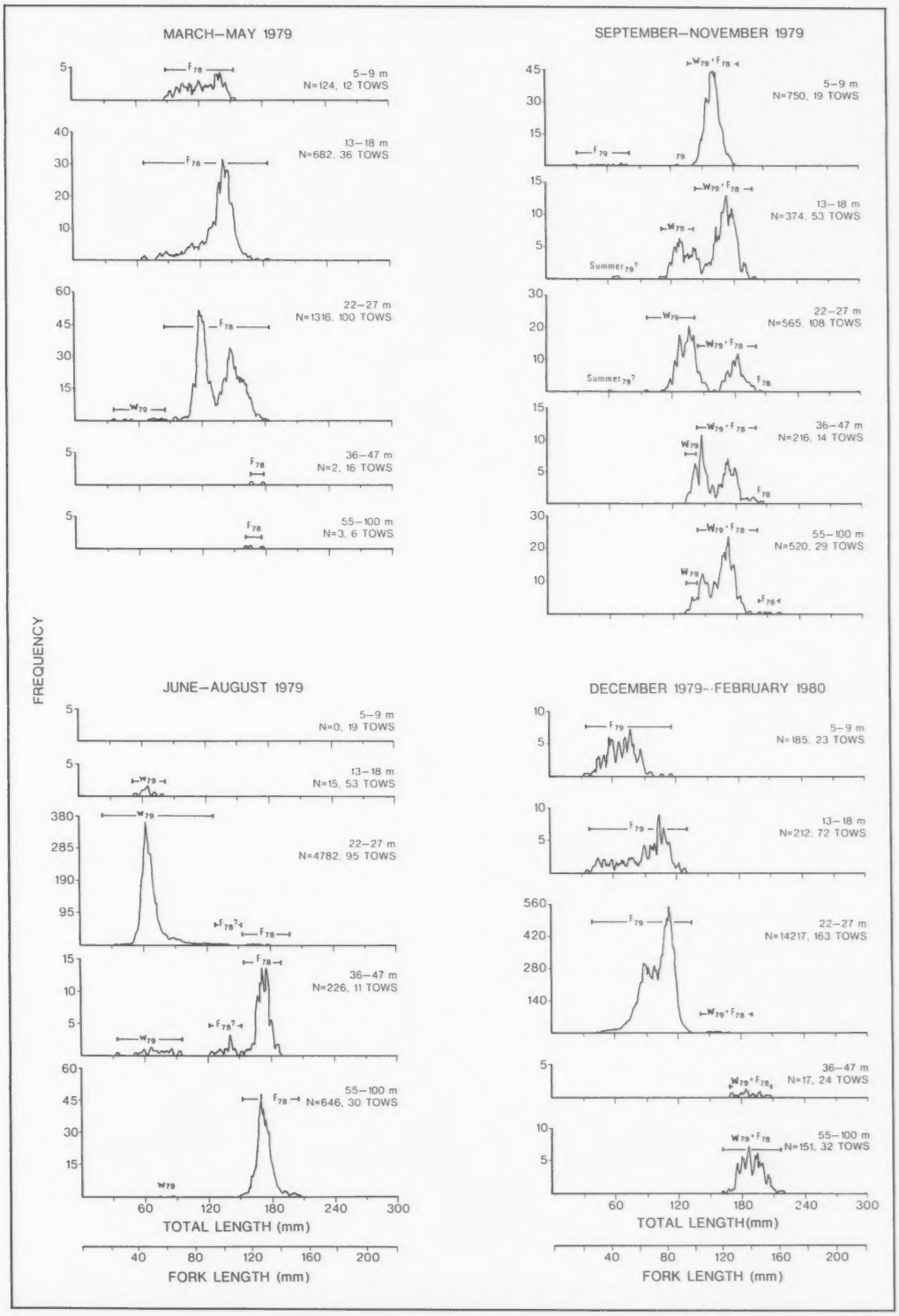
Growth and age determination by length frequency

Length frequencies could be used to determine age of *P. burti* through at least 13–16 months of age in the northwestern Gulf and apparently 20–27 months of age in the northcentral Gulf. No more than two cohorts occurred off Texas in any one month, except in March and December 1978, November 1979 through January 1980, and May through June 1980 when a few members of a third group were present (Fig. 4). Each cohort was followed easily until it disappeared when 13–16 months old. In contrast, in the northcentral Gulf in April 1980 there were three cohorts west of the Mississippi River and four to the east (Fig. 7). Fish were abundant at 20 months of age west of the Mississippi and were as old as 27 months to the east (Table 3).

Early sizes for *P. burti* average 25 mm in length at 1 month of age, 42 mm at 2 months, 57 mm at 3 months, 72 mm at 4 months, and 84 mm at 5 months. These values are predicted from quadratic regressions of length-on-age in days pooling all Winter and Fall cohorts (Table 2). Similar size-age combinations may be predicted from quadratic regressions for individual cohorts, and for pooled Winter groups and pooled Fall groups.

Peprilus burti average about 65–100 mm in length at 6 months, 120–145 at age I, and about 170 mm at age II, but fish in the northcentral Gulf were smaller at age than off Texas. Quadratic and von Bertalanffy growth equations both fit observed data from off Texas well, and they predict similar sizes-at-age over most of the observed size range (Fig. 8). For Winter fish quadratic and von Bertalanffy equations predicted lengths of 99 and 100 mm at 6 months, respectively, and 146 and 141 mm at age I (Fig. 8). Observed lengths show many Winter fish were as large as 120 mm at 6 months and 155 mm at age I (Fig. 4; Murphy 1981, Table 1). For Fall fish, quadratic and von Bertalanffy equations predict lengths of 93 and 97 mm at 6 months, respectively, and 131 and 130 mm at age I. Observed lengths show many Fall fish were as large as 105 mm at 6 months and 145 mm at age I. Winter-spawned fish from the northcentral Gulf averaged 120–124 mm at

Figure 6 (facing page)
Length frequencies of *Peprilus burti* by depth: March–May 1979, June–August 1979, September–November 1979, December 1979–February 1980.


MARCH–MAY 1979
5–9 m
N=124, 12 TOWS
13–18 m
N=682, 36 TOWS
22–27 m
N=1316, 100 TOWS
36–47 m
N=2, 16 TOWS
55–100 m
N=3, 6 TOWS
SEPTEMBER–NOVEMBER 1979
5–9 m
N=750, 19 TOWS
13–18 m
N=374, 53 TOWS
22–27 m
N=565, 108 TOWS
36–47 m
N=216, 14 TOWS
55–100 m
N=520, 29 TOWS
JUNE–AUGUST 1979
5–9 m
N=0, 19 TOWS
13–18 m
N=15, 53 TOWS
22–27 m
N=4782, 95 TOWS
36–47 m
N=226, 11 TOWS
55–100 m
N=646, 30 TOWS
DECEMBER 1979–FEBRUARY 1980
5–9 m
N=185, 23 TOWS
13–18 m
N=212, 72 TOWS
22–27 m
N=14217, 163 TOWS
36–47 m
N=17, 24 TOWS
55–100 m
N=151, 32 TOWS
FREQUENCY
TOTAL LENGTH (mm)
TOTAL LENGTH(mm)
FORK LENGTH (mm)

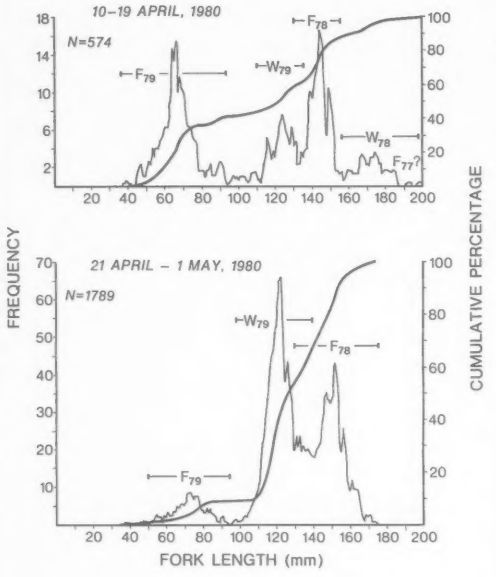


Figure 7

Length-frequency and cumulative percentages of *Peprilus burti* from the northcentral Gulf, (top) east and (bottom) west of the Mississippi River, April–May 1980. Cohort identities are indicated.

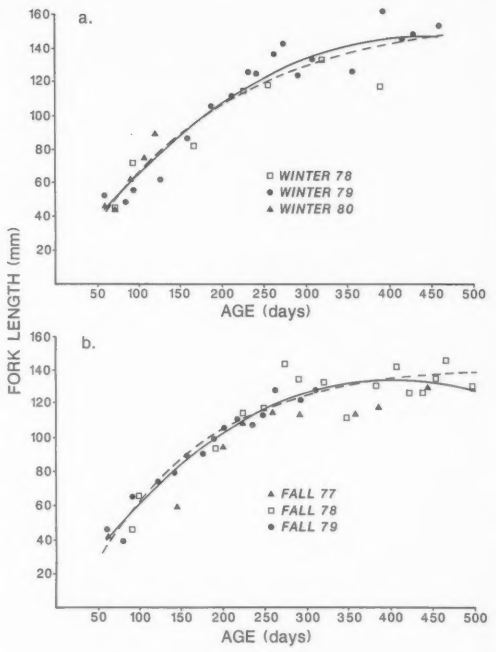


Figure 8

Mean observed and predicted sizes-at-age of Winter and Fall cohorts of *Peprilus burti* off Freeport, Texas. Predicted sizes were estimated for pooled Winter and Fall data from regressions of mean sizes-on-age using quadratic (solid line) and von Bertalanffy growth (dashed line) models. Regressions were significant at $\alpha = 0.05$.

13 months and 171 mm at 27 months (Table 3). Fall-spawned fish averaged 66–73 mm at 7 months and 142–149 mm at 20 months.

Male and female *P. burti* reach a similar size off Texas. The largest male sexed was 173 mm and the largest female was 163 mm. Both sexes were equally abundant among fish greater than 150 mm.

Peprilus burti showed little apparent somatic growth off Texas as spawning approached, but fish from the northcentral Gulf had large annual growth increments. Off Texas, fish grew little after reaching modal sizes of 110–160 mm at 7–15 months in Winter groups and 120–150 mm at 9–16 months of age in Fall groups (Figs. 4, 8). Growth ceased or greatly slowed between

Table 3

Size-at-age (mm FL) data for *Peprilus burti* from the northcentral Gulf, east and west of the Mississippi River. Ages assume hatching dates assigned to cohorts off Freeport, Texas.

Spawned group	Approx. age (mo.)	West of Mississippi River			East of Mississippi River		
		n	Size range	Mean FL	*n*	Size range	Mean FL
$Fall_{79}$	7	150	50–95	73	235	37–93	66
$Fall_{78}$	20	743	132–176	149	196	130–155	142
$Fall_{77}$	33	0	—	—	0	—	—
$Winter_{79}$	13	1029	98–139	120	105	110–135	124
$Winter_{78}$	27	0	—	—	61	155–200	171
$Winter_{77}$	38	0	—	—	0	—	—

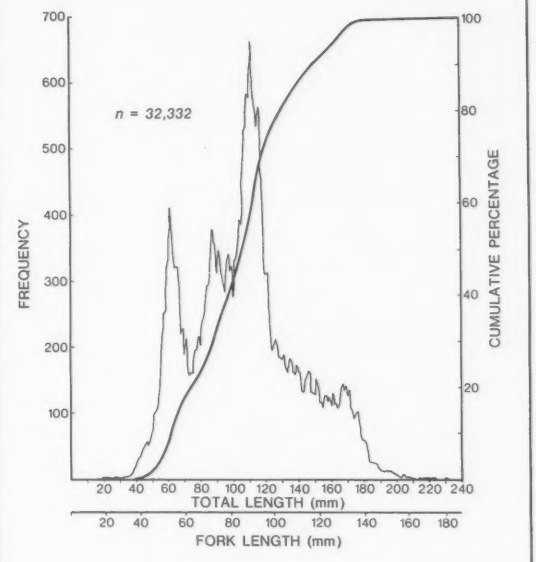


Figure 9
Length-frequency and cumulative percentage of *Peprilus burti* off Freeport, Texas.

the Late Developing and Ripe stages when sizes formed a plateau (Fig. 2). In contrast, growth of Winter and Fall cohorts in the northcentral Gulf continued for fish 7–13 months of age and 20–27 months of age (Table 3).

Maximum size and age

The maximum size of *P. burti* is about 200 mm in length. The largest of 32,332 fish we captured off Texas was only 180 mm, though a 198 mm specimen was measured among only 574 fish from the northcentral Gulf east of the Mississippi River (Fig. 7). Off Texas, 90% of the fish were less than 122 mm, 99% were less than 142 mm, and 99.5% were less than 145 mm (Fig. 9).

The maximum age of *P. burti* typically was only 1–1.5 years in the northwestern Gulf but appeared to be 2–2.5 years in the northcentral Gulf where the largest individuals occur. A t_L of 1–1.5 years seems reasonable off Texas, because fish larger than 142–145 mm, which made up less than 0.5–1.0% of the catch, approximate the average size there at age I. A larger t_L is appropriate for the northcentral Gulf (Fig. 7), because 99–99.5% of the fish west of the Mississippi River were less than 163–167 mm long and 99–99.5% of those to the east were less than 182–184 mm. These sizes approximate the average at age II in the northcentral Gulf and the oldest fish collected there was about age II, so a reasonable estimate of t_L is 2–2.5 years.

Total weight-length, girth-length, and length-length relationships

Regressions of total weight on fork length (Table 4) were significantly different (at $\alpha = 0.05$) in elevation between sexes ($F = 9.19$, 1, 1615 df) but not in slope ($F = 3.25$, 1, 1614 df). Calculated slopes did not significantly differ from $\beta = 3.0$ (males: $t = 0.97$, 789 df; females: $t = 1.60$, 825 df) except when all fish were pooled ($t = 20.08$, 2734 df). Girth-fork length and length-length regressions are in Table 4.

Table 4
Weight-length, girth-length, and total, fork, and standard length regressions for *Peprilus burti*. All regressions were significant at $\alpha = 0.05$. Measures are grams and millimeters.

Equation	n	FL range	r^2
$\log_{10}$ TW = −4.5517 + 2.9640 $\log_{10}$ FL (males)	791	100–163	0.89
$\log_{10}$ TW = −4.7095 + 3.0477 $\log_{10}$ FL (females)	827	94–164	0.93
$\log_{10}$ TW = −4.8621 + 3.1201 $\log_{10}$ FL (males, females, immatures)	2736	25–164	0.99
G = 10.38 + 0.99 FL	2736	25–164	0.95
FL = −4.31 + 0.96 G	2736	25–164	0.95
FL = 8.35 + 0.73 TL	2662	25–164	0.99
TL = −9.35 + 1.35 FL	2662	26–164	0.99
SL = 3.22 + 0.69 TL	2668	25–164	0.99
TL = −2.88 + 1.42 SL	2668	25–164	0.99
FL = 5.05 + 1.05 SL	2734	25–164	0.99
SL = −4.46 + 0.95 FL	2734	25–164	0.99

Discussion

Spawning periodicity and its regulation

The broad primary spawning period of September through May we suggest for *Peprilus burti* is realistic. Our data agrees with reports of fish 20–40 mm in length from December through June (Gunter 1945, Hoese 1965, Miller 1965) and, in part, with a suggested fall and winter spawning (Miller 1965). Moreover, Finucane et al. (1979) collected larvae off Texas from September through May.

We interpret our data to mean *P. burti* spawns primarily—or most successfully—in temporally separate, discrete, Winter (late January–mid-May), and Fall (early September–late October) periods. The consistently well-separated, bimodal length frequencies—on which we place great emphasis—must reflect a temporal separation in spawning activity or success, or growth and mortality, that originates during late fall and early winter. However, the well-developed gonads and Gravid/Ripe fish we observed suggest spawning could occur throughout that period, possibly at a low level. Allen et al. (1986) and Vecchione (1987) also found consistently bimodal size distributions of *P. burti* in the northcentral Gulf. Allen et al. (1986) considered them separate spawning peaks in a continuous, not temporally separated, spawning. The actual degree of temporal separation in spawning of *P. burti* may be important to resolve, because it may influence (1) appropriate management practices, (2) how many populations and stocks exist in *P. burti*, concepts which are not necessarily the same, and (3) how speciation occurs in *Peprilus*. Given properly randomized geographical sampling, age determination by daily otolith increments (Jones 1986) might resolve the question of how intense is late-fall to early-winter spawning and whether or not, and to what degree, spawning is temporally separate.

Although *P. burti* appear to spawn primarily in two main periods, Winter and Fall, it also appears that in each period there is much variation in cohort spawning periodicity or success, or in recruitment periodicity. We observed Winter cohorts to appear as distinct abundant groups in April in one year but not until June in two other years. Similarly, one Fall cohort was distinctly bimodal over a several-month time period. A more exact method of age determination than length frequencies, however, is needed to more clearly interpret these phenomena.

Our interpretation of spawning periodicity in *P. burti* is similar to findings that other Gulf species spawn in discrete Winter–Spring and Late Summer–Fall periods related to current transport, including *Cynoscion arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), *Larimus fasciatus* (Standard and Chittenden 1984), *Menticirrhus americanus* (Harding and Chittenden 1987), and *Polydactylus octonemus* (Dentzau and Chittenden 1990). Spawning of *P. burti* in the northwestern Gulf, and for many of these other fishes, probably is timed to coincide with currents (Shlossman and Chittenden 1981) that transport eggs and larvae from spawning areas to nurseries, assuming *P. burti* has pelagic eggs and larvae like *P. alepidotus* and *P. triacanthus* (Martin and Drewry 1978). Spawning, or its absence, coincides with wind-induced, up- or downcoast, alongshore coastal currents which drive circulation in the northwestern Gulf with seasonal reinforcement from the Mississippi—Atchafalaya discharge (Kelly et al. 1981). Average winds are downcoast (toward Mexico) during August/September–April/May but upcoast (toward Florida) during May/June–July/August. Nearshore currents parallel the coast. Upcoast wind stress causes upcoast alongshore currents which (1) are reflected in high inshore salinity off Galveston/Freeport and falling sea levels during early to midsummer (Marmer 1954, Kelly et al. 1981), and (2) coincide with the summer period of little spawning we observed in *P. burti* and which is reported in other species just cited. Downcoast wind stress causes downcoast (toward Mexico) alongshore currents, onshore surface Ekman transport, and downwelling which (1) are reflected in rising sea levels February–May and August–October, (2) transport low-salinity water downcoast causing a salinity minimum off Galveston/Freeport during September and October, and May and June, and (3) coincide with the two major spawning periods we suggest for *P. burti* and which are reported as major or minor periods in other species just cited. Alongshore currents continue downcoast from late fall to early winter. Seemingly, however, no distinct, abundant groups of *P. burti* originated then, which may reflect low-level spawning or spawning success. Similarly, little or no spawning occurs then in the other species just cited. Temporal variation in the average meteorological and hydrographic patterns may be the primary reason for the variation we noted in cohort spawning and recruitment periodicity between and within years.

Age determination and growth, maximum size and age, and mortality

Our findings on age and growth in *P. burti* are new, because this species has not been aged previously. It would be desirable to corroborate them by analysis of daily otolith increments (Jones 1986). However, that may not prove feasible, because recent studies using scales, opercula, vertebrae, and thin-sectioned otoliths, fail to consistently show clear daily increments or annuli (Allen et al. 1986). Therefore, it appears length frequencies are the only way to age *P. burti* at present. As in our study, supporting length collections must be frequent in time and over a long duration, because cohort boundaries and age are not clear every month. However, they are quite clear in certain months (for examples, the $Winter_{79}$ and $_{80}$ groups in May or June 1979 and 1980, the $Fall_{78}$ and $_{79}$ groups in December 1978 and 1979). From the clear groups, one can work chronologically backward and forward in time and gradually assign age and cohort boundaries with reasonable certainty. This process, however, is not as

simple in species with a complex life history like *P. burti* as it is in species that spawn during one major period a year.

The apparent cessation of somatic growth as *P. burti* approach spawning in the northwestern Gulf contrasts with large annual increments in the northcentral Gulf. This difference, combined with their disappearance from the northwestern Gulf at 13–16 months of age and their smaller maximum sizes and younger maximum ages there (see below), indicate fish from the northwestern Gulf (1) spawn and die at age I, or more probably (2) in some presently unclear combination emigrate offshore and to the northcentral Gulf prior to, or immediately after, spawning.

Few *P. burti* apparently exist larger than 190–200 mm in length. The largest we captured (180 mm, Texas; 198 mm, northcentral Gulf) are similar to maxima in other studies' sampling to at least 80–100 m depths (173 mm, Hildebrand 1954; 184 mm, Franks et al. 1972; 169 mm, Chittenden and McEachran 1976; 193 mm, Allen et al. 1986). Maxima are even smaller from estuaries or the shallow Gulf (154 mm, Gunter 1945; 131 mm, Miller 1965; 122 mm, Perret et al. 1971; 133 mm, Christmas and Waller 1973), which agrees with our findings that *P. burti* disperse to deep water as they mature. The largest records were from the northcentral Gulf (Allen et al. 1986; our study).

Our estimate that $t_L = 1$–1.5 years in the northwestern Gulf agrees with Chittenden and McEachran (1976) who suggested a 1–2 year maximum age. A higher t_L (2–2.5 years) in the northcentral Gulf appears realistic, because the largest records there are not much larger than the mean size at age II. Based on these maximum ages, theoretical estimates (Royce 1972, Hoenig 1983) of total annual mortality rate ($1 - S$) are nearly 100% in the northwestern Gulf and 82–90% in the northcentral Gulf. Murphy (1981) calculated similar values of $1 - S$ for the northwestern Gulf (99%) from observed time-specific abundance data for consecutive Winter or Fall cohorts. If mature fish from the northwestern Gulf emigrate offshore and to the northcentral Gulf, as we suggest, our values for maximum age and total mortality are under- and overestimates, respectively, for *P. burti* in the northwestern Gulf.

The presence of the largest *P. burti* in the northcentral Gulf follows a pattern in other marine and estuarine, demersal and pelagic species (*Cynoscion nothus*, DeVries and Chittenden 1982; *Stenotomus caprinus*, Geoghegan and Chittenden 1982; *Micropogonias undulatus*, Rivas and Rothmayr 1970, Gutherz et al. 1975, White and Chittenden 1977; *Brevoortia patronus*, Nicholson 1978; *Larimus fasciatus*, Standard and Chittenden 1984; and probably *C. arenarius*, Shlossman and Chittenden 1981). Small differences between areas also exist in other population attributes of *P. burti*, as in *C. nothus* and *L. fasciatus*: younger age compositions and maximum ages, smaller maximum sizes, and higher total annual mortality rates occur in the northwestern Gulf. At least three explanations could account for this: (1) There may be no basic differences between areas, just much greater biomass (Moore et al. 1970) at age in the northcentral Gulf; (2) differences may be real, not related to biomass, implying slight, but fundamental, population dynamics differences between areas; and (3) differences reflect some presently unclear combination of an offshore and spawning or postspawning movement of older, larger fish from the northwestern to the northcentral Gulf. The first implies Chittenden and McEachran (1976) and Chittenden (1977) are correct that shrimp communities on the Gulf continental shelf have a common population dynamics pattern. The other explanations imply that their arguments need modification for slightly longer life spans and lower mortality rates in the northcentral Gulf, and that shrimp communities are a little more sensitive to fishing than Chittenden's (1977) simulations indicate.

Movements, recruitment, and spawning areas

Peprilus burti probably spawn offshore. We found fish congregate in 36–100 m depths as they mature and size gradients that indicate an offshore dispersal. In agreement, Allen et al. (1986) found a positive correlation between mean size and depth at 200–290 m. Finucane et al. (1979) collected larvae in water 22–182 m deep on the continental shelf off Texas. The young make their way inshore to 5–27 m depths off Freeport, Texas—the white shrimp community (Hildebrand 1954, Chittenden and McEachran 1976)—where they recruit to the bottom. At least two mechanisms could explain their arrival inshore. For one, Ekman surface transport, associated with prevailing downcoast alongshore currents in the spawning season, could, in theory, bring the young inshore. However, Dentzau and Chittenden (1990) rejected this idea. It implies fishes of the brown shrimp community would also recruit inshore, but, in actuality, there is a clear separation between the two communities (Chittenden and McEachran 1976). A more likely alternative, suggested for *Polydactylus octonemus* (Dentzau and Chittenden 1990), is based on the hydrography and cyclonic gyre of the northwestern Gulf (Kelly et al. 1981, 1983, 1984): The eastward counterflow of the gyre is diverted inshore at the Mississippi River delta and ultimately extends downcoast as an alongshore current. Members of the white shrimp community could spawn anywhere in this flow, in the offshore northeastward flowing arc or in the

alongshore southwestward flow: the young just need to be entrained in waters already in the white shrimp community, or enter them using the eastward counterflow, and be transported in a "downstream manner" (see next paragraph). This interpretation is similar to the current transport model Shaw et al. (1985) suggest for *B. patronus*.

Besides being offshore, spawning grounds for *P. burti* found off Texas may lie towards or in the northcentral Gulf. We suggest some unknown combination of offshore and spawning or postspawning movement to the northcentral Gulf explains between-area population dynamics differences. Such upcoast movement may be required within the white shrimp community, given the coincidence of spawning with downcoast currents. Mean alongshore surface current speed is 23 cm/second in water 22 m deep off Freeport, Texas from September through June (Kelly et al. 1981), so spawning areas could lie 320 nmi upcoast assuming passive transport for 30 days before the young recruit to the bottom. This estimate depends on many poorly known factors, including (1) routes followed, (2) alongshore current speeds, (3) duration of the transport period, and (4) behavior of the young. However, alongshore currents could transport young great distances—conceptually "downstream"—and Texas recruits could be spawned off Louisiana where low-salinity waters propagate along Texas when alongshore wind components turn downcoast during August and September (Kelly and Randall 1980, Kelly et al. 1981). Mature fish must move toward spawning areas, conceptually in an upstream, contranatant direction from the northwestern Gulf, to maintain a fixed, proven spawning ground following Harden Jones (1968).

Zoogeographic considerations

Peprilus burti fill a niche in the Gulf similar to the one *P. triacanthus* occupies on the Atlantic coast. However, their population dynamics differ, and this may reflect zoogeographic variation suggested for other taxa whose ranges traverse the Cape Hatteras area, including *Micropogonias* and *Alosa* (White and Chittenden 1977), *Cynoscion* (Shlossman and Chittenden 1981), and *Stenotomus* (Geoghegan and Chittenden 1982). It appears for *P. burti* that (1) maturity occurs at 100–160 mm in length as they approach age I and spawn, (2) maximum size is only about 200 mm, but most are much smaller, (3) maximum age is no more than 2.5 years, and (4) total annual mortality rate is not lower than about 82%.

The life history of *P. triacanthus* north of Cape Hatteras is complicated by north–south and onshore–offshore movements (Horn 1970), but they appear to (1) mature at lengths of 110–130 mm in their second year (Hildebrand and Schroeder 1927, Bigelow and Schroeder 1953, Horn 1970, DuPaul and McEachran 1973), (2) reach maximum sizes of 300 mm (Murawski and Waring 1979), (3) have maximum ages of 3–6 years (Draganik and Zukowski 1966, DuPaul and McEachran 1973, Waring 1975, Kawahara 1977), and (4) have total annual mortalities of 67–84% (Murawski and Waring 1979).

Little has been published for *P. triacanthus* south of Cape Hatteras, but the largest fish collected in extensive trawling in this area was 150 mm (Wenner et al. 1979). This size range is more similar to *P. burti* than *P. triacanthus* north of Cape Hatteras and may reflect an intrageneric, Carolinian Province similarity in sizes, maximum ages, and mortality.

Acknowledgments

We are much indebted to M. Burton, T. Crawford, P. Geoghegan, J. Pavela, M. Rockett, J. Ross, P. Shlossman, B. Slingerland, G. Standard, H. Yette, and Captains Hollis, Mike, and Robby Forrester, P. Smirch, and A. Smircic for assistance in field collections. T. Fehrman and R. Grobe recorded the data. R. Case was of invaluable help for writing and assisting with computer programs. B. Rohr and E. Gutherz allowed the senior author to participate in NMFS groundfish survey 106. R. Darnell, G. Grant, E. Klima, D. Stilwell, K. Strawn, and K. Sulak reviewed drafts of the manuscript. Financial support was provided, in part, by the Texas Agricultural Experiment Station; by the Strategic Petroleum Reserve Program, Department of Energy; and by the Texas A&M Sea Grant College Program, supported by the NOAA Office of Sea Grant, U.S. Department of Commerce. Final preparation and revisions of this manuscript were made while the authors were at Florida Marine Research Institute, Florida Department of Natural Resources (MDM) and College of William and Mary, Virginia Institute of Marine Science (MEC). This manuscript was based on a thesis submitted by the senior author as partial fulfillment of the M.S. degree, Texas A&M University.

Citations

Allen, R.L., J.H. Render, A.W. Liebzeit, and G.W. Bane
1986 Biology, ecology, and economics of butterfish and squid off the northern Gulf of Mexico. Final Rep. LSU-CFI-86-30, Coastal Fish. Inst., Center for Wetland Resources, Louisiana State Univ., Baton Rouge, 175 p.

Alverson, D.L., and M.J. Carney
1975 A graphic review of the growth and decay of population cohorts. J. Cons. Cons. Int. Explor. Mer 36:133–143.

Bagenal, T.B., and E. Braum
1971 Eggs and early life history. *In* Ricker, W.E. (ed.),

Methods for assessment of fish production in fresh waters, p. 166–198. Blackwell Sci. Publ., Oxford.

Bigelow, H.B., and W.C. Schroeder
1953 Fishes of the Gulf of Maine. Fish. Bull., U.S. 53(74), 577 p.

Caldwell, D.K.
1961 Populations of the butterfish, *Poronotus triacanthus* (Peck), with systematic comments. Bull. South. Calif. Acad. Sci. 60:19–31.

Chittenden, M.E. Jr.
1977 Simulations of the effect of fishing on the Atlantic croaker, *Micropogon undulatus*. Proc. Gulf Caribb. Fish. Inst. 29:68–86.

Chittenden, M.E. Jr., and J.D. McEachran
1976 Composition, ecology, and dynamics of demersal fish communities on the northwestern Gulf of Mexico continental shelf, with a similar synopsis for the entire Gulf. Sea Grant Publ. TAMU-SG-76-208, Texas A&M Univ., College Station, 104 p.

Christmas, J.Y., and R.S. Waller
1973 Estuarine vertebrates, Mississippi. *In* Christmas, J.Y. (ed.), Cooperative Gulf of Mexico estuarine inventory and study, Mississippi, p. 320–434. Gulf Coast Res. Lab., Ocean Springs, MS, 434 p.

Collette, B.B.
1963 The systematic status of the Gulf of Mexico butterfish, *Poronotus burti* (Fowler). Copeia 1963:582–583.

Dentzau, M.W., and M.E. Chittenden Jr.
1990 Reproduction, movements, and apparent population dynamics of the Atlantic threadfin, *Polydactylus octonemus*, in the Gulf of Mexico. Fish. Bull., U.S. 88:439–462.

DeVries, D.A., and M.E. Chittenden Jr.
1982 Spawning, age determination, longevity, and mortality of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico. Fish. Bull., U.S. 80:487–500.

Draganik, B., and Cz. Zukowski
1966 The rate of growth of butterfish, *Peprilus triacanthus*, and ocean pout, *Macrozoarces americanus*, from the region of Georges Bank. Int. Comm. Northwest Atl. Fish. Res. Doc. 66/42, 3 p.

DuPaul, W.D., and J.D. McEachran
1973 Age and growth of the butterfish, *Peprilus triacanthus*, in the lower York River. Chesapeake Sci. 14:203–207.

Finucane, J.H., L.A. Collins, L.E. Barger, and J.D. McEachran
1979 Environmental studies of the South Texas outer continental shelf, 1977: Ichthyoplankton/mackerel eggs and larvae. Final Rep. to Bur. Land Manage., by Natl. Oceanic Atmos. Admin., Interagency Agreement AASSO-1A7-21. Galveston Lab., Natl. Mar. Fish. Serv., NOAA, Galveston, TX 77550, 504 p. (avail. NTIS, Springfield, VA).

Franks, J.S., J.Y. Christmas, W.L. Siler, R. Combs, R. Waller, and C. Burns
1972 A study of the nektonic and benthic faunas of the shallow Gulf of Mexico off the State of Mississippi. Gulf Res. Rep. 4, 148 p.

Gallucci, V.F., and T.J. Quinn III
1979 Reparameterizating, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108:14–25.

Geoghegan, P., and M.E. Chittenden Jr.
1982 Reproduction, movements, and population dynamics of the longspine porgy, *Stenotomus caprinus*. Fish. Bull., U.S. 80:523–540.

Gledhill, C.T.
Unpubl. A preliminary estimate of Gulf butterfish (*Peprilus burti*) MSY and economic yield. Mississippi Lab., Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Pascagoula, MS, 16 p.

Gulland, J.A.
1969 Manual of methods for fish stock assessment. Part I. Fish population analysis. FAO Manuals in Fish. Sci. 4, 154 p.

Gunter, G.
1945 Studies on marine fishes of Texas. Publ. Inst. Mar. Sci., Univ. Tex. 1, 190 p.

Gutherz, E.J., G.M. Russell, A.F. Serra, and B.A. Rohr
1975 Synopsis of the northern Gulf of Mexico industrial and foodfish industries. Mar. Fish. Rev. 37(7):1–111.

Harden Jones, F.R.
1968 Fish migration. Edw. Arnold Publ., Ltd., London, 325 p.

Harding, S.M., and M.E. Chittenden Jr.
1987 Reproduction, movements, and population dynamics of the southern kingfish, *Menticirrhus americanus*, in the northwestern Gulf of Mexico. NOAA Tech. Rep. NMFS 49, 21 p.

Hildebrand, H.H.
1954 A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. Publ. Inst. Mar. Sci., Univ. Tex. 3:103–109.

Hildebrand, S.F., and W.C. Schroeder
1927 Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43 (pt. 1), 388 p.

Hoenig, J.M.
1983 Empirical use of longevity data to estimate mortality rates. Fish. Bull., U.S. 82:898–903.

Hoese, H.D.
1965 Spawning of marine fishes in the Port Aransas, Texas area as determined by the distribution of young and larvae. Ph.D. diss., Univ. Tex., Austin, 144 p.

Horn, M.H.
1970 Systematics and biology of the stromateoid fishes of the genus, *Peprilus*. Bull. Mus. Comp. Zool. Harv. Univ. 140: 165–261.

Jearld, A. Jr.
1983 Age determination. *In* Nielson, L.A., and D.L. Johnson (eds.), Fisheries techniques, p. 301–324. Am. Fish. Soc., Bethesda, MD.

Jones, C.
1986 Determining age of larval fish with the otolith increments technique. Fish. Bull., U.S. 84:91–103.

Kawahara, S.
1977 Age and growth of butterfish, *Peprilus triacanthus* (Peck), in the ICNAF subarea 5 and statistical area 6. Int. Comm. Northwest Atl. Fish. Res. Doc. 77/VI/27, 13 p.

Kelly, F.J. Jr., and R.E. Randall
1980 Physical oceanography. *In* Hann, R.W. Jr., and R.E. Randall (eds.), Evaluation of brine disposal from the Bryan Mound site of the Strategic Petroleum Reserve Program. Final report of predisposal studies, p. 1–93. Contract DOE/P010114-2, Texas A&M Univ., College Station (avail. NTIS, Springfield, VA).

Kelly, F.J., J.E. Schmitz, R.E. Randall, and J.E. Cochrane
1981 Physical oceanography. *In* Hann, R.W. Jr., and R.E. Randall (eds.), Evaluation of brine disposal from the Bryan Mound site of the Strategic Petroleum Reserve Program. Final report of twelve-month post-disposal studies, p. 1–105. Contract DOE/P010114-4, Texas A&M Univ., College Station (avail. NTIS, Springfield, VA).
1983 Physical oceanography. *In* Hann, R.W. Jr., and R.E. Randall (eds.), Evaluation of brine disposal from the Bryan Mound site of the Strategic Petroleum Reserve Program: Annual report for September 1981 through August 1982, p. 1–134. Contract DOE/P010114-6, Texas A&M Univ., College Station (avail. NTIS, Springfield, VA).

1984 Physical oceanography. *In* Hann, R.W. Jr., C.P. Giammona, and R.E. Randall (eds.), Offshore oceanographic and environmental monitoring services for the Strategic Petroleum Reserve: Annual report for the Bryan Mound Site from September 1982 through August 1983, p. 1–122. Contract DOE/P010850-2, Texas A&M Univ., College Station (avail. NTIS, Springfield, VA).

Knight, W.
1968 Asymptotic growth: An example of nonsense disguised as mathematics. J. Fish. Res. Board Can. 25:1303–1307.

Lagler, K.F.
1956 Freshwater fishery biology, 2d ed. Wm. C. Brown Co. Publ., Dubuque, Iowa, 421 p.

Marmer, H.A.
1954 Tides and sea level in the Gulf of Mexico. *In* Galtsoff, P.S. (ed.), Gulf of Mexico, its origin, water and marine life, p. 101–118. Fish. Bull., U.S. 89, 604 p.

Martin, F.D., and G.E. Drewry
1978 Development of fishes of the mid-Atlantic Bight, Vol. VI. U.S. Fish Wildl. Serv. Biol. Serv. Prog. FWS/OBS-78/12, 416 p.

Miller, J.M.
1965 A trawl study of the shallow Gulf fishes near Port Aransas, Texas. Publ. Inst. Mar. Sci., Univ. Tex. 10:80–108.

Moore, D., H.A. Brusher, and L. Trent
1970 Relative abundance, seasonal distribution, and species composition of demersal fishes off Louisiana and Texas, 1962–1964. Contrib. Mar. Sci., Univ. Tex. 15:45–70.

Murawski, S.A., and G.T. Waring
1979 A population assessment of butterfish *Peprilus triacanthus*, in the northwestern Atlantic Ocean. Trans. Am. Fish. Soc. 108:427–439.

Murphy, M.D.
1981 Aspects of the life history of the Gulf butterfish, *Peprilus burti*. M.S. thesis, Texas A&M Univ., College Station, 76 p.

Nicholson, W.R.
1978 Gulf menhaden, *Brevoortia patronus*, purse seine fishery, catch, fishing activity, and age and size composition, 1964–1973. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 722, 8 p.

Perret, W.S., W.R. Latapie, J.F. Pollard, W.R. Mock, G.B. Adkins, W.F. Gaidry, and C.J. White
1971 Fishes and invertebrates. *In* Perret, W.S. (ed.), Cooperative Gulf of Mexico inventory and study, Louisiana. Phase IV, Biology, p. 39–197. La. Fish. Wildl. Comm., Baton Rouge.

Perschbacher, P.W., K.J. Sulak, and F.J. Schwartz
1979 Invasion of the Atlantic by *Peprilus burti* (Pisces: Stromateidae) and possible implications. Copeia 1979: 538–541.

Rivas, L.R., and C.M. Roithmayr
1970 An unusually large Atlantic croaker, *Micropogon undulatus*, from the northern Gulf of Mexico. Copeia 1970: 771–772.

Rohr, B.A., A.J. Kemmerer, and W.H. Fox Jr.
1980 FRS *Oregon II* Cruise 106 4/10-5/1/80, Cruise Report. Mississippi Lab., Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Pascagoula, MS, 12 p.

Roithmayr, C.M.
1965 Industrial bottomfish fishery of the northern Gulf of Mexico, 1959–63. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 518, 23 p.

Royce, W.F.
1972 Introduction to the fishery sciences. Academic Press, NY, 351 p.

Saila, S.B., C.W. Reckseik, and M.H. Prager
1988 Basic fishery science programs, a compendium of microcomputer programs and manual of operation. Elsevier Sci. Publ., NY, 230 p.

Shaw, R.F., W.J. Wiseman Jr., R.E. Turner, L.J. Rouse Jr., R.E. Condrey, and F.J. Kelly Jr.
1985 Transport of larval gulf menhaden *Brevoortia patronus* in continental shelf waters of western Louisiana: A hypothesis. Trans. Am. Fish. Soc. 114:452–460.

Shlossman, P.A., and M.E. Chittenden Jr.
1981 Reproduction, movements, and population dynamics of the sand seatrout, *Cynoscion arenarius*. Fish. Bull., U.S. 79:649–669.

Standard, G.W., and M.E. Chittenden Jr.
1984 Reproduction, movements, and population dynamics of the banded drum, *Larimus fasciatus*, in the Gulf of Mexico. Fish. Bull., U.S. 82:337–363.

Tesch, F.W.
1971 Age and growth. *In* Ricker, W.E. (ed.), Methods for assessment of fish production in fresh waters, 2d ed., p. 98–130. Blackwell Sci. Publ., Ltd., London.

Vecchione, M.
1987 Commercial fishing for gulf butterfish, *Peprilus burti*, in the Gulf of Mexico. Mar. Fish. Rev. 49(4):14–22.

Waring, G.
1975 A preliminary analysis of the status of the butterfish in ICNAF subarea 5 and statistical area 6. Int. Comm. Northwest Atl. Fis. Res. Doc. 75/74, 27 p.

Wenner, C.A., C.A. Barans, B.W. Stender, and F.H. Berry
1979 Results of MARMAP otter trawl investigations in the South Atlantic Bight. III. Summer, 1974. Tech. Rep. 41, S.C. Mar. Resour. Cent., Charleston, 62 p.

White, M.L. and M.E. Chittenden Jr.
1977 Age determination, reproduction and population dynamics of the Atlantic croaker, *Micropogonias undulatus*. Fish. Bull., U.S. 75:109–123.

Impact of Compensatory Responses on Assessment Advice for the Northwest Atlantic Mackerel Stock

William J. Overholtz
Steven A. Murawski
William L. Michaels

Woods Hole Laboratory, Northeast Fisheries Science Center
National Marine Fisheries Service, NOAA, Woods Hole, Massachusetts 02543

Abstract.– Annual assessments of the Northwest Atlantic mackerel stock have occurred every year since 1973, providing useful advice to fishery managers involved in the decision making process for this important pelagic resource. Since 1985, assessment advice based on an $F_{0.1}$ management strategy has indicated that catches in the 300,000 mt range are feasible because stock biomass has increased greatly after the collapse of the fishery in the mid-1970s. However, indications from previous research are that compensatory processes are very important, so a stochastic simulation model with density-dependent growth, maturity, and natural mortality was constructed to study how these mechanisms might affect our ability to provide short- and long-term advice for this important stock. Model results suggest that our present assessments may be too optimistic relative to yield projections and that minimum spawning-stock biomass levels may be difficult to maintain even with an $F_{0.1}$ fishing strategy. Model results also reveal that natural mortality rates are probably much higher than previously thought and are important in determining trends in abundance in this stock.

Manuscript accepted 19 September 1990.
Fishery Bulletin, U.S. 89:117–128 (1991).

The Northwest Atlantic stock of Atlantic mackerel *Scomber scombrus* has historically been important to the U.S. domestic fishery; records from the early 1800s to the 1980s suggest that cumulative landings have been 7–8 million mt over that time-period (Sette and Needler 1934, Hoy and Clark 1967, Anderson 1985). A thriving domestic industry utilized mackerel well into the 1940s until landings dropped because of declines in abundance, availability, and increased production of fresh and frozen white fish products (e.g., haddock, cod) (Hoy and Clark 1967, Jenson 1967). A resurgence of the fishery occurred in the 1970s when distant water fleets from eastern Europe and the Soviet Union landed an average of 310,000 mt annually from 1970 to 1976 (Fig. 1A). Since many of the important groundfish species in the region have declined recently, the U.S. industry has become more interested in mackerel as a volume (high-catch, low-price) fishery.

The fishery has been managed under the auspices of the Mid-Atlantic Fishery Management Council since 1977. Current management objectives for this stock include maintenance of a minimum spawning stock (600,000 mt), annual quotas based on an $F_{0.1}$ catch strategy and a recognition of the necessity for keeping the total stock at some reasonably high level to insure that the recreational fishery remains viable.

Recent assessments suggest that the stock has increased since collapsing in the late 1970s. A succession of moderate to good year-classes from 1981 to 1985 promoted rapid recovery of the stock to levels observed in the early 1970s (Fig. 1B, C). Assessment advice during the last several years based on an $F_{0.1}$ management strategy has indicated that annual catches in the 300,000 mt range are feasible in the short term. Allocations to joint ventures have increased over the last several years, amounting to about 75,000 mt in 1987, but recent landings have remained well below the 300,000 mt level and fishing mortality has averaged only about 0.07 since 1980 (Overholtz and Parry 1985).

Pelagic fishes such as mackerel are important in the trophic dynamics of fishery ecosystems, supporting populations of predatory fish, birds, and marine mammals. Additionally, these species may also increase to densities that inhibit their own population processes (e.g., growth, reproduction) and those of competitors. Evidence exists that Atlantic mackerel exhibit density-dependent growth (McKay 1979, Lett 1980, Overholtz 1989). Other factors such as maturation rates, fecundity-at-age, and predation mortality rates may also vary

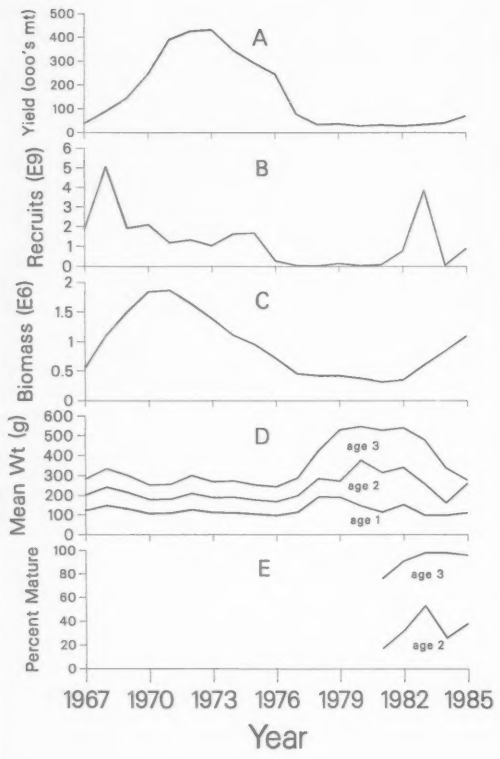


Figure 1

Descriptive data for the Northwest Atlantic mackerel stock, 1967–85. (A) Yield (ooo's mt); (B) Recruitment at age 1 (billions of fish); (C) Spawning-stock biomass (ooo's mt); (D) Mean weight at ages 1, 2, and 3 from commercial samples (g); (E) Percent maturity for ages 2 and 3.

with stock size. An analysis of the food habits of mackerel predators suggested that natural mortality rates (M2) for this stock were higher during 1973–75 when relatively large numbers of juvenile mackerel were available, and declined during 1976–80 when there were few small fish (NEFC 1987).

This study examines the impact that compensatory changes in growth, sexual maturity, and natural mortality rates may have on the Northwest Atlantic mackerel stock. Implications of responses in these factors on catch and spawning-stock biomass are evaluated using a simulation model. The model was designed so that changes in these compensatory factors as well as the influence of fishing mortality patterns and strategies could be assessed.

Model background

Data on potential density-dependent population regulatory mechanisms were obtained from research vessel survey cruises and commercial fishing operations conducted on the U.S. eastern coast. Information from spring groundfish surveys conducted by the Northeast Fisheries Center (NEFC) during 1973–85 and a commercial fishery conducted by Poland during 1981–86 were examined to quantify compensatory relationships. Analyses were performed to study changes in growth, maturation rates, and natural mortality (Overholtz et al. 1988, Overholtz 1989).

Significant negative relationships between mean weight-at-age and stock size were confirmed for both research and commercial data sources (Overholtz et al. 1988, Overholtz 1989). Mean size-at-age for recent year-classes was also found to be significantly different; large year-classes grew more slowly (Overholtz 1989). In addition mean weight-at-age was also negatively related to year-class size, indicating that large cohorts may depress growth rates of individuals from that particular year (Overholtz 1989) (Fig. 1D). These analyses helped us to quantify the relationship between growth and density for this stock in our modeling exercises.

Maturity data from 1981–86 were evaluated to ascertain if percent maturity at age 2 and 3 changed over the time period. No fish were mature at age 1, and all fish were mature at age 4+ (Overholtz et al. 1988). Percent maturity at age 2 ranged from 17% in 1981 to 53% in 1983 (Fig. 1E). Percent mature at age 3 ranged from 67% in 1986 to 98% in 1983 and 1984 (Overholtz et al. 1988) (Fig. 1E).

The maturity data were collected in conjunction with age sampling and were not a priority item. During the critical time of gonadal development in mid- to late April, maturity samples were often sparse because age sampling requirements had been fulfilled; no additional maturity samples were collected because of this. A cursory examination of the data revealed that there was an apparent negative relationship with increased stock size at age 2 and no consistent pattern at age 3 (Overholtz et al. 1988) (Fig. 1). The null hypothesis of no impact of density on maturity rates could not be accepted or rejected with the data at hand; we therefore included this potential mechanism in our modeling studies to ascertain its overall importance.

During 1967–85 the northwest Atlantic mackerel stock underwent profound changes in recruitment with a subsequent decline in biomass (Fig. 1B, C). We considered this a good time period to study changes in predation on mackerel and associated possible changes in natural mortality rates (M). For the purposes of discussion in this paper we define natural mortality rate (M = M1 + M2), where M1 = sources of natural mortal-

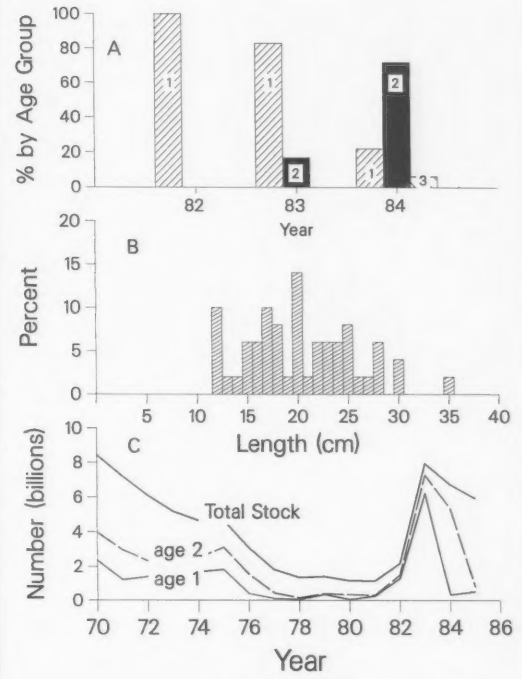


Figure 2

(A) Percent by age group of Atlantic mackerel sampled as prey in Atlantic cod, silver hake, and spiny dogfish stomachs in 1982 (n = 8), 1983 (n = 12), 1984 (n = 32). (B) Length frequency of mackerel sampled in Atlantic cod, silver hake, and spiny dogfish stomachs, 1982–84. (C) Cumulative numbers of ages 1 and 2, and the total stock of mackerel from VPA stock size estimates for 1970–85.

Table 1

Percentage of mackerel by weight in stomach samples of silver hake, Atlantic cod, and spiny dogfish, and number of stomachs collected for 1973–76 and 1977–80.

	1973–76		1977–80	
Species	%	*N*	%	*N*
Silver hake	4.21	2622	0.82	1657
Cod	11.50	1009	0.10	457
Spiny dogfish	3.30	389	0.10	2662

ity other than predation, and M2 = predation mortality (ICES 1987). Since there was no multispecies virtual population analysis (MSVPA) available to examine annual trends in predation mortality rates (M2), we decided to use another method to examine possible changes in M2. We wanted to investigate possible predation mortality models for mackerel for this period of time.

Summaries of NEFC food habits data indicate that spiny dogfish *Squalus acanthias*, Atlantic cod *Gadus moruha*, and silver hake *Merluccius bilinearis* are the most important fish predators on mackerel (Langton and Bowman 1980, Bowman and Michaels 1984, Bowman et al. 1984). Food habits data were collected from 1973 to 1980, but did not include individual lengths of prey items from these predators. However, maximum, minimum, and average lengths of fish prey were recorded. Almost all the mackerel consumed in these years were less than 30 cm (Overholtz et al. 1988).

To study the problem in more detail, food habits data from 1982–84 were examined to determine the size and age distribution of mackerel as prey items in the three fish predators. These data were chosen since detailed records of predator and prey length were available. Mackerel up to 35 cm were taken as prey by the three species, but fish 30 cm or less composed the bulk of the prey. These fish were predominantly ages 1 and 2 from the 1981–83 year-classes (Fig. 2A, B). Mackerel appeared to be consumed roughly in proportion to their abundance in the sea during 1982–84 (Fig. 2A, C).

Our analysis thus centered on predation by these three predators on age-1 and -2 mackerel. Total food consumed (all species) by each predator was calculated and the average percentage of mackerel by weight comprising the diet of each predator was estimated separately for the periods 1973–76 and 1977–80 (Table 1). A period average was used because there was not enough information available for annual estimates. These two time-periods were chosen because the design of the food-habits sampling regime was different in each period, and because the abundance of small mackerel was much different in each of the periods (Fig. 2C).

The method used to calculate consumption was based on residence times of the predator and prey, percent by weight of mackerel in the predator diet, daily ration estimates for the predator by season, if available, abundance of 1- and 2-year-old mackerel in the sea, and biomass of predators of the correct size distribution (Bowman et al. 1984, Rexstad and Pikitch 1986). This method assumed that the estimate of predator biomass was an appropriate measure of the average standing stock present during the year, that mackerel consumed were only age-1 and -2 fish, and that predators consumed mackerel relative to their abundance in the sea. The estimates were made for 1973–80 for each predator species and the total number of age 1- and -2 fish consumed annually was estimated (Table 2).

Total consumption of mackerel by each predator was calculated as

$$C_i = B_i \cdot \%BW \cdot \%Rm_i \cdot Tr \quad (1)$$

where

C_i = consumption of mackerel by predator i,
B_i = biomass of predator i,
%BW = daily ration estimate,
%Rm = percent of total ration composed of mackerel for predator i,
Tr = residence time of predator and prey (days), and
i = 1,3.

The estimated consumption in weight was then converted to numbers eaten on the basis of information on the abundance of age-1 and -2 mackerel in the sea and the mean weights of each age group. Consumption estimates were combined with landings-at-age for 1973–80 and a new VPA was completed for these years (Overholtz et al. 1988). A residual natural mortality rate (M1) of 0.20 was used in this analysis to account for other sources of mortality at ages 1 and 2 and for all the other age groups (3–14) in the analysis. A similar assumption has been used by ICES in the multispecies VPA model of the North Sea (ICES 1987). The mortality rates from the VPA were a proxy for F and M2 and were apportioned by using the ratios of consumption and landings to total deaths (numbers). This gave an estimate of F and M2 mortalities for 1973–80 (Table 3). Consumption (numbers) of age-1 mackerel exceeded landings of that age group in all years from 1973 to 1980 and was generally smaller than landings at age 2 (Table 2). Sizes of incoming year-classes increased up to a factor of two in the revised VPA over the 1973–80 period (Overholtz et al. 1988). When mortality rates from the VPA were apportioned by consumption estimates and landings, natural mortality rates (M = M1 + M2) were generally higher in the 1973–76 period, when mackerel were abundant, than in 1977–80 (Table 3).

These values and the new VPA stock size-at-age estimates were used in regressions to study the relationship between M2 and year-class strength. The results of this analysis suggest a positive relationship between M2 for ages 1 and 2 and year-class size (R = 0.37, 0.78, P = 0.363, 0.0234), respectively (Fig. 3A, B). An examination of the scatter plots from these two regressions revealed that the M2 value from 1976 was high relative to the number of age-1 and -2 fish in the stock. There were fewer age-1 fish in the stock in 1976 (Fig. 2C); furthermore, food habits data indicated that mackerel was not present in the diet of the three predators in 1976. The 1976 data point was dropped and a new regression was fitted for age 1 (R = 0.60, P = 0.157, Fig. 3A).

We were cognizant of the fact that results of this analysis may have been influenced by the assumption of proportional feeding. However, the suggestion that natural mortality rates may change with year-class size is an interesting research question. A positive relationship between year-class size and predation mortality rate has obvious implications for assessment and management, and thus the potential impacts of density-dependent predation mortality were a major focus of our modeling studies.

Table 2
Annual consumption of age-1 and -2 Atlantic mackerel by spiny dogfish, silver hake, and Atlantic cod, landings of mackerel for 1973–80, and total for both categories (millions of fish).

	Consumption		Landings		Total	
Year	Age 1	Age 2	Age 1	Age 2	Age 1	Age 2
1973	590.0	224.1	161.8	283.2	751.8	507.3
1974	823.0	135.1	95.9	242.2	918.9	377.3
1975	616.0	170.0	373.7	431.4	989.7	601.4
1976	202.8	278.3	12.5	353.5	215.3	631.8
1977	8.4	15.1	2.0	27.0	10.4	42.1
1978	11.1	6.6	0.1	0.2	11.2	6.8
1979	14.1	1.2	0.4	0.6	14.5	1.8
1980	6.1	8.4	1.2	10.9	7.3	19.3

Table 3
Mortality rates of age-1 and -2 Atlantic mackerel for 1973–80.

	Age 1				Age 2			
Year	Z	F	M2	M1	Z	F	M2	M1
1973	0.78	0.12	0.46	0.20	0.75	0.31	0.24	0.20
1974	0.66	0.05	0.41	0.20	0.86	0.42	0.24	0.20
1975	0.71	0.19	0.32	0.20	0.83	0.45	0.18	0.20
1976	0.81	0.04	0.57	0.20	0.93	0.41	0.32	0.20
1977	0.40	0.04	0.16	0.20	0.42	0.14	0.08	0.20
1978	0.61	0.00	0.41	0.20	0.39	0.01	0.18	0.20
1979	0.30	0.00	0.10	0.20	0.31	0.04	0.07	0.20
1980	0.44	0.04	0.20	0.20	0.38	0.10	0.08	0.20

Model structure

A simulation model addressing changes in growth, percent maturity-at-age, and predation mortality rates

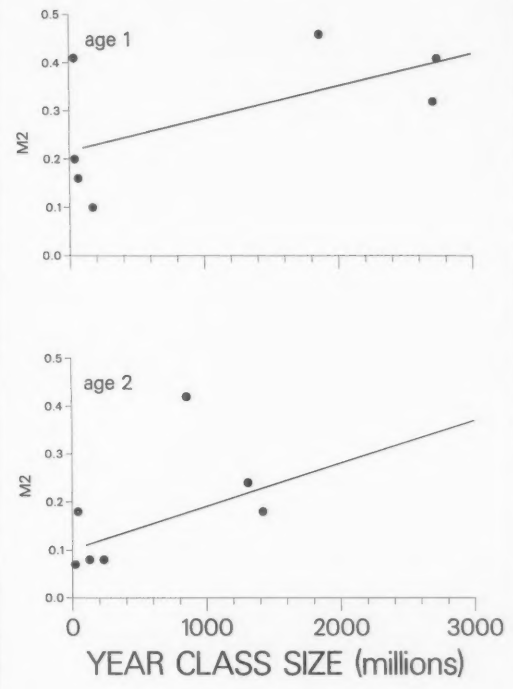


Figure 3
Relationship between predation mortality (M2) and year-class size for age-1 and -2 Atlantic mackerel from calculations of mackerel consumption by Atlantic cod, silver hake, and spiny dogfish for 1973–80.

(M2) was constructed to evaluate the potential impact of these population regulatory mechanisms in the context of single-species assessment advice. The model was a basic fishery simulator much in the same style as many other common fishery models (Walters 1969, Sissenwine 1977). An age-structured Baranov catch equation was used to compute annual fishery yields, and the negative exponential relationship was used to update stock size for 14 age groups.

A stochastic recruitment function was used to model recruitment for the mackerel stock. A three-parameter model (Shephard 1982; Table 4) with a lognormal white-noise multiplier was used to generate an annual estimate of recruitment as:

$$R = (a * SSB)/[1 + (SSB/K)^b] * lnm \quad (2)$$

where R = recruitment at age 1,
SSB = spawning-stock biomass,

Table 4
Parameters used in stochastic simulations of the Atlantic mackerel stock; e-4 = 10^{-4}, e-5 = 10^{-5}, e-6 = 10^{-6}.

	age	a	b	K
Weight (Wt_1)	1	0.122	−1.24e-5	—
Growth (G_i)	2	0.187	−1.42e-5	—
increment	3	0.154	−1.08e-5	—
	4	0.132	−1.03e-5	—
	5	0.102	−8.62e-6	—
Recruitment (R)	1	5.800	1.7	600.0
Maturity (PM)	2	0.543	−2.14e-4	—
	3	1.043	−2.14e-4	—
Predation	1	0.600	3.00	2.5
mortality (M2)	2	0.500	2.00	2.5

a, b, K = parameters,
lnm = lognormal multiplier with u and s from the SR data.

Recruitment estimates were scaled upward by a factor of 1.5 to account for the fact that the original VPA age-1 stock size estimates do not reflect higher natural mortality rates due to predation (Overholtz et al 1988).

Growth-at-age was based on a two-stage model that related life-history characteristics and year-class size to growth increment for a year-class (Overholtz 1989). Since age-1 fish maintain a separate distribution from the adult stock (Sette 1950) a relationship between age-1 growth and corresponding age-1 year-class size was used to predict weight at age 1. The relationship was parameterized (Table 4) with available empirical data, such that size at age 1 varied from 48 g for slow-growing fish to 122 g for fast-growing fish (Overholtz 1989). Weight of age-1 mackerel was calculated as

$$Wt_1 = a - bN_1 \quad (3)$$

where Wt = average weight (g) at age,
N_1 = year-class size at age 1 (numbers),
a, b = parameters.

Age 2–5 growth was determined by relationships between adult stock size (numbers) and growth-at-age (Table 4) calculated as

$$Wt_i = Wt_{i-1} + G_i \quad (4)$$

where Wt_i = average weight at age i, i = 2, 5,
G_i = annual age-specific growth increment (g),

and

$$G_i = a_i - b_i SS \quad (5)$$

where SS = total adult stock size (numbers),
a,b = age specific parameters.

The increment from ages 2 to 5 was smaller the larger the adult stock. Fish weight at ages 1–5 was the result of growth in the first year and subsequent increments at ages 2–5; thus, age-1 growth partially determined the average weight of a fish throughout its lifetime. If the stock was reduced in any given year, the cohort could recover and grow faster. Growth at ages 6+ was assumed to follow trends in the recent data, since by this time cumulative mortality has usually been sufficient to reduce a cohort to lower levels.

Percent maturity at ages 2 and 3 was assumed to vary based on a relationship between the fraction mature and spawning stock size calculated as

$$PM_i = a - b(SSB) \quad (6)$$

where PM_i = percent mature at age i, i = 2,3,
SSB = spawning-stock biomass,
a,b = parameters.

This submodel was parameterized (Table 4) so that the maturity of age-2 fish can vary from 20 to 50%, while maturities for age-3 fish range from 70 to 100%.

Natural mortality due to predation (M2) for ages 1 and 2 fish was estimated from a relationship between M2 and year-class size-at-age (Fig. 4; Table 4) calculated as

$$M2_i = (a * YC_i)/[1 + (YC_i/K)^b] \quad (7)$$

where $M2_i$ = natural mortality due to predation on age i, i = 1,2,
YC_i = year-class size at age i, i = 1,2,
a,b,K = parameters.

M2 mortalities on age-1 and -2 fish could reach approximately 1.0 and 0.6, respectively, with this model.

This relationship was used since it approximates the findings of our mortality study over an initial range of stock size (Fig. 3A, B), and since it appears to be an appropriate predator prey response model (Holling 1965, Murdoch 1973). Although this model does not produce a typical type-3 response (Holling 1965) exactly, since there is no inflection point over the initial stock sizes (Fig. 4), it serves as a sufficient functional model to study the natural mortality mechanism.

The density-dependent simulation model (DDM) was used to study the impact of different levels of fishing mortality, management strategies, and to investigate hypotheses concerning the role of compensatory responses in regulating this stock. Monte Carlo simulations were produced for a variety of different scenarios, and average results from 1000 annual data points were summarized. Results from the model were compared with forecasts from the current standard assessment model (STD).

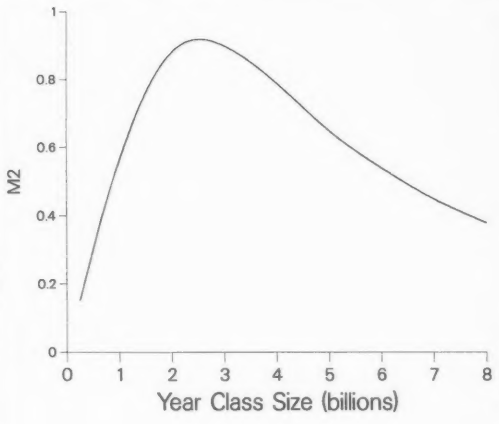


Figure 4
Type 3 functional relationship between predation mortality rate (M2) and year-class size used in the density-dependent simulation model (DDM).

Model sensitivity and validation

The sensitivity of model results to the different density-dependent mechanisms was investigated by comparing catch in 1987 and spawning stock in 1988 and 1991 for all the different combinations of growth, maturity, and natural mortality at a reference fishing mortality of 0.05. In runs where only a single mechanism was examined, 1987 catch was most affected by changes in the growth pattern (mean weights) of the stock (Fig. 5-B). Spawning stock in 1988, on the other hand, was almost equally sensitive to maturity and natural mortality. Density-dependent natural mortality influenced 1991 spawning stock to the greatest degree (Fig. 5-C).

When the results of pairing the mechanisms were examined, weight and natural mortality had the greatest effect on catch, percent maturity, and natural mortality on SSB in 1988 and weight and natural mortality on SSB in 1991 (Fig. 5-D, E, F). When the three mechanisms were all operating there was no change in the impact on 1987 catch, but spawning stock in 1988 and 1991 was several percentage points lower (Fig. 5-G).

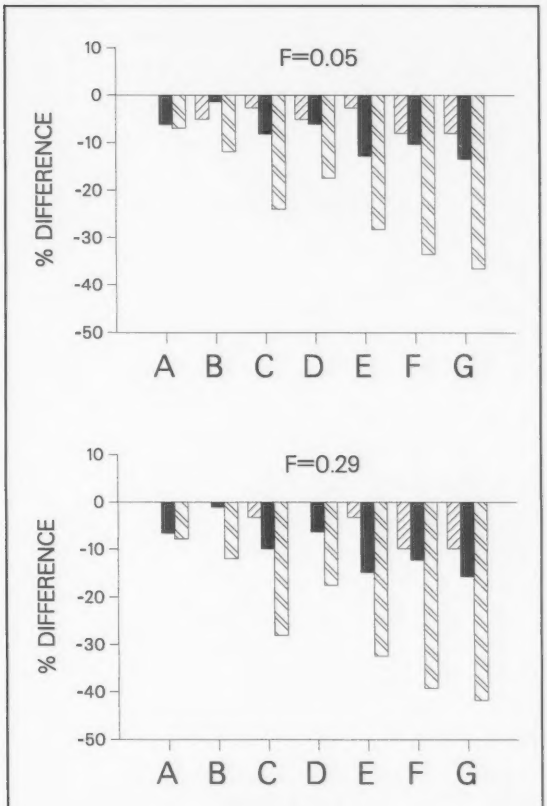


Figure 5

Impact on 1987 catch, 1988 spawning-stock biomass (SSB), and 1991 SSB of running the density-dependent simulation (DDM) model with all possible combinations of growth, maturity, and predation mortality. (A) maturity; (B) growth; (C) predation mortality; (D) growth, maturity; (E) maturity, predation mortality; (F) growth, predation mortality; (G) maturity, growth, predation mortality.

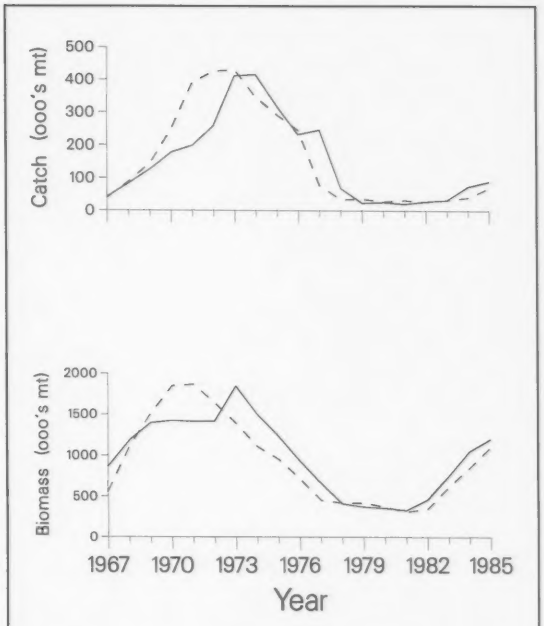


Figure 6

Comparison of observed (– – –) catch and biomass versus simulated (——) catch and biomass obtained from running the density-dependent simulation (DDM) model with historic estimates of fishing mortality, historic recruitment estimates scaled by a factor of 1.5, and density-dependent growth, maturity, and predation mortality.

A validation run of the density-dependent model was produced for comparison with the observed time-series of catch and VPA biomass for 1967–85 (Fig. 6). The simulated series was produced by using the same fishing mortality series as in the VPA, recruitment scaled upward by a factor of 1.5, and density-dependent growth, maturity, and natural mortality. The pattern of simulated versus observed catch and biomass is quite comparable in terms of trend and magnitude, except for a few years in the early 1970s. This occurs even though the density-dependent model has greatly different natural mortality rates at ages 1 and 2 and much higher recruitment. Another run with the same F pattern, recruitment scaled by 1.5, and no density dependence produced the same trend in catch and biomass for 1967–85, but the values were approximately a factor of two larger than the observed series. Thus, not including the density-dependent component resulted in values of catch and SSB that were greatly different than the observed series.

The model components were validated by comparing the different outputs produced by the various mechanisms with available empirical data. In some cases, relationships were re-parameterized or tuned to produce results in the same ranges as observed in the empirical database. The model was used to investigate a variety of different problems. Runs from the STD model were compared with the results of the different density-dependent model outputs to gauge the changes that occurred in catch, total stock, spawning stock, mean weights, and other factors. STD runs were parameterized with the same data as that used in the 1986 assessment (Overholtz et al 1988).

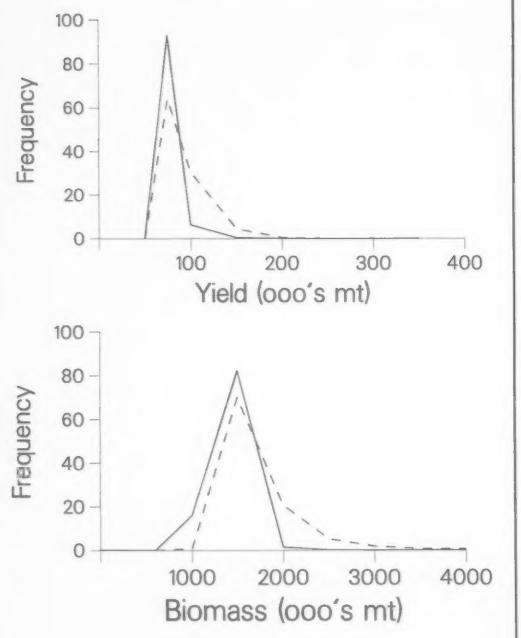


Figure 7
Comparison of standard assessment (STD) model (– – –) and density-dependent simulation (DDM) model (——) catch and spawning-stock biomass (SSB) for 5000 iterations of each model, with fishing mortality set at 0.05.

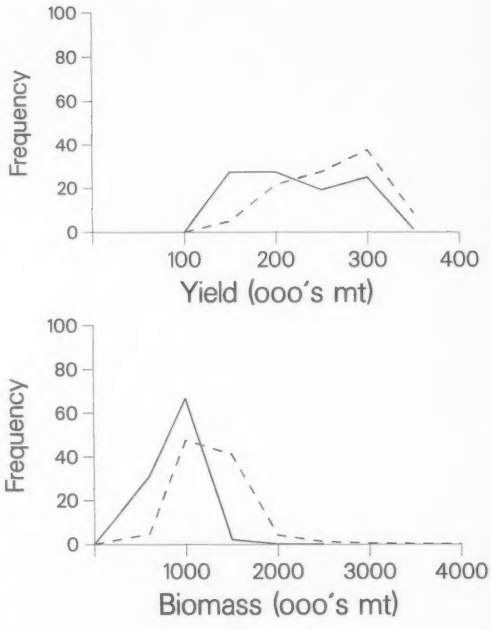


Figure 8
Comparison of standard assessment (STD) model (– – –) and density-dependent simulation (DDM) model (——) catch and spawning-stock biomass (SSB) for 5000 iterations of each model, with fishing mortality set at 0.29 ($F_{0.1}$).

Model results

Short-term perspective

Since fishing mortality has been so low in recent years and the stock has increased, an attempt was made to investigate the effect of further stockpiling of fish on expected catches and spawning stock size. To address this problem, a series of 5-year simulations were used to compare the density-dependent model results with projections from the standard model. Fishing mortality was set at 0.05, a value close to the average rate over the last several years. These runs suggest that advice based on the standard model would have overpredicted catch by about 8% in 1987 and spawning stock size in 1988 by about 13% (Fig. 5-G). Furthermore, if the standard model were used to project more than a few years into the future, the estimate of spawning stock could possibly be too large; the 1991 estimate would be lower by 37% for the DDM model (Fig. 5-G). If the frequency of yields over this 5-year series is calculated, the STD model is more optimistic with a mean catch of 74,892 mt versus 63,686 mt for the DDM model (Fig. 7). Similarly for spawning-stock biomass (SSB), the STD model suggests a higher mean SSB of 1.5 million mt versus 1.1 million mt for the DDM model (Fig. 7).

Since $F_{0.1}$ is an important benchmark fishing-mortality rate in the present management plan, another 5-year summary with $F = 0.29$ ($F_{0.1}$) was also produced. As with the previous example, mean yield for the STD model was considerably higher, 242,939 mt versus 197,116 mt for the DDM model (Fig. 8). Spawning-stock biomass would be considerably different under the two perspectives with an estimated mean SSB of 1.0 million mt under the STD model and 725,887 mt under the DDM model (Fig. 8).

Long-term perspective

To develop a longer-term perspective, simulations at the same two levels of fishing mortality ($F = 0.05, 0.29$) were produced for 15-year series to allow sufficient

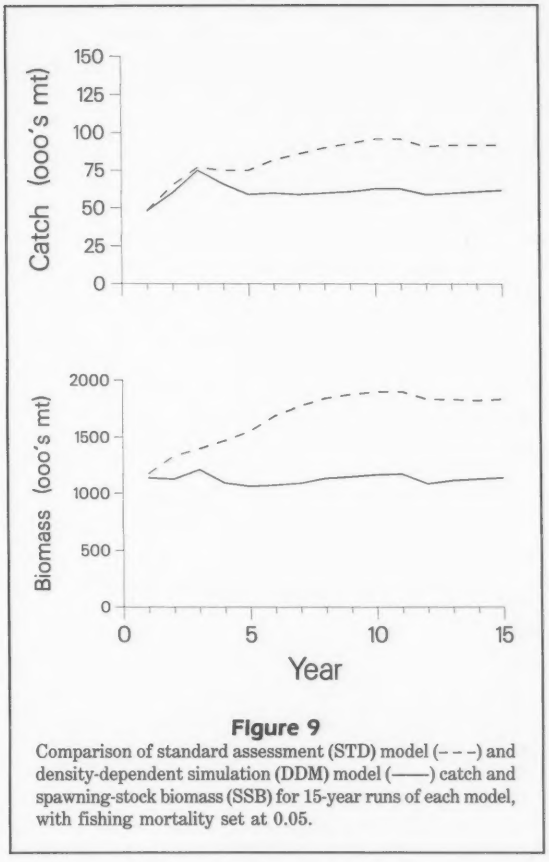


Figure 9
Comparison of standard assessment (STD) model (- - -) and density-dependent simulation (DDM) model (——) catch and spawning-stock biomass (SSB) for 15-year runs of each model, with fishing mortality set at 0.05.

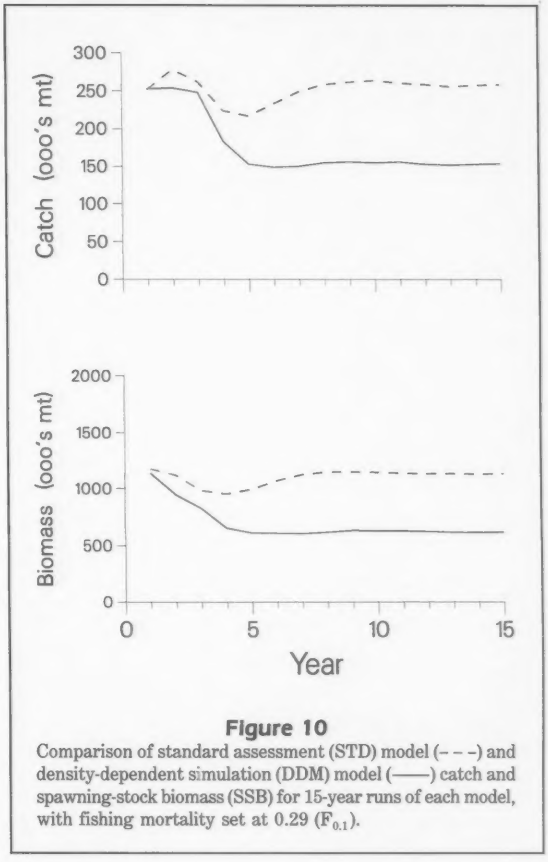


Figure 10
Comparison of standard assessment (STD) model (- - -) and density-dependent simulation (DDM) model (——) catch and spawning-stock biomass (SSB) for 15-year runs of each model, with fishing mortality set at 0.29 ($F_{0.1}$).

time for the stock to reach an equilibrium point. At F = 0.05, and after roughly 7–8 years, catch would be higher under the STD model than for the DDM model (Fig. 9). Spawning-stock biomass would also be considerably higher, about 1.7 million mt for the STD model versus about 1.1 million mt for the DDM model (Fig. 9).

Fishing the stock at $F_{0.1}$ for a 15-year period would result in an equilibrium catch of roughly 250,000 mt (STD) versus 150,000 mt (DDM) after about 7–8 years (Fig. 10). The spawning stock would appear to be much higher, 1.1 million mt versus 615,000 mt, for the STD and DDM models, respectively (Fig. 10).

To evaluate the overall differences between the two models, two measures of performance and one measure of risk were produced for fishing mortality values ranging from 0.1 to 0.6, in 0.1 increments for a total of 1000 runs of each model. Mean catch, coefficient of variation (CV) of catch, and proportion of time the spawning stock fell below 600,000 mt, the management plan benchmark, were calculated for year 10 of the simulation. Based on the previous model runs, the tenth year of the simulation appeared to be a reasonable choice for a summary year (Figs. 9, 10).

Mean catch would continue to increase dramatically under the STD model until F reached about 0.40 and would remain relatively constant thereafter. Yields would also steadily increase for the DDM model at F's ranging from 0.1 to 0.3, but would remain constant after that point (Fig. 11A). A comparison of expected yields under the two models suggests that the STD model is always more optimistic, especially at the higher levels of fishing mortality (Fig. 11). Mean catch at F = 0.5 would be about 125,000 mt higher under the STD model.

Variability as measured by CV's of the catch increased with increases in fishing mortality for the STD model, but remained relatively constant at about 50% for the DDM model. Thus the STD model is more optimistic at lower levels of fishing mortality and becomes

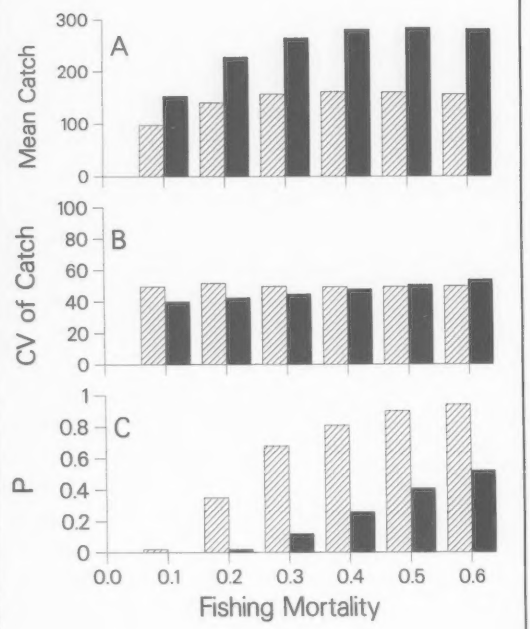


Figure 11

(A) Mean catch, (B) coefficient of variation of catch, and (C) proportion of the time spawning-stock biomass (SSB) falls below 600,000 mt for year 10 of a set of 10-year simulations of the standard assessment (STD) (darkened bar) and density-dependent simulation (DDM) (cross-hatched bar) models, with fishing mortalities of 0.1–0.6 in 0.1 increments.

progressively more variable as fishing mortality increases (Fig. 11B). Both models have relatively high CV's at all levels of fishing mortality, suggesting a large range in possible catches.

The minimum spawning-stock criteria of 600,000 mt is a threshold biomass defined in the present fishery management plan. This value was chosen by managers because a relatively clear demarcation point between low and high recruitment is evident in the 1962–85 stock-recruit data series (Anderson 1985). When the simulation results are expressed relative to the proportion of times the SSB drops below the 600,000 mt level for each model, the STD model appears to be much less prone to risk and, therefore, is much more optimistic than the DDM model results. The proportion ranges from 0.0 at F = 0.1 to about 0.52 at F = 0.6 for the STD model, while P ranges from 0.01 to 0.94 for the DDM model (Fig. 11C). The STD model results suggest that there is little risk of the SSB dropping below the threshold, even at fishing mortality rates of 0.4–0.5 (Fig. 11C). The DDM model results are much less optimistic, suggesting the need for some concern at fishing mortality levels of 0.3 and greater (Fig. 11C).

Discussion

Biological interactions may play an important role in regulating marine ecosystems (Sherman et al. 1981, Walters et al. 1986, Overholtz and Tyler 1986, Overholtz et al. In press). Species interactions are becoming an important fishery management issue, and assessment advice is increasingly contingent on these mechanisms (Anderson and Ursin 1977; Pope 1976, 1979; Shephard 1984; ICES 1987,1988). This study indicates that the stock dynamics of Atlantic mackerel are not only influenced by fishing, but that predation and intraspecific compensatory mechanisms including density-dependent growth are strong influences that probably effect yield forecasts and management advice in the short and long term.

Large differences in mackerel growth suggest that year-class size partially influences the initial pattern of growth during a cohort's first several years. Adult stock size probably plays an important role in regulating growth after a year-class recruits to the adult portion of the population (Overholtz 1989). Declines in growth are probably significant as stock biomass increases (Overholtz 1989). Model results, although not presented in this paper, suggest that mackerel would reach a larger size if the mackerel stock were fished more heavily. Larger catches of Atlantic mackerel would probably cause growth to stabilize at higher rates, and more of the annual production would be available for harvest.

Predation mortality rate has usually not been accounted for in the past in most assessment work, but recent studies have shown the importance of including this mechanism to enhance stock assessments (Anderson and Ursin 1977; Shephard 1984; ICES 1987,1988; Overholtz et al. 1990). Our analysis suggests that predation probably has a major influence on the dynamics of Northwest Atlantic mackerel. Predation mortality is probably the largest component of natural mortality on this stock, since other sources such as general diseases, parasitism, and epizootics are not thought to be important sources of mortality on most fish stocks on an annual basis (Anderson 1979). Strong year-classes of mackerel may attract elevated levels of predation, in contrast with the usual assumption of constant natural mortality. Other studies have suggested that predation mortality rates should continually decline or remain constant as abundance increases (Sparre 1984). Our model results indicate that preda-

tion mortality rates on Atlantic mackerel are probably much higher than previously thought.

The results of the model projections show that unless the impacts of compensatory mechanisms are accounted for, evaluations of current stock status using the current standard assessment methodology may, in fact, be optimistic and risky if catches are increased to high levels in the future (Fig. 11). The differences in results between the two models are, of course, contingent on the parameterizations of the growth and predation mortality submodels and how recruitment is scaled in the density-dependent model. Two advances in research on mackerel would help to improve our ability to assess the stock: An MSVPA to provide correctly scaled estimates of recruitment, and a general predation mortality model that would provide useful estimates of M2's for forecasting purposes. Although recent assessment advice indicates that catches can be increased on the mackerel stock (Overholtz and Parry 1985), it perhaps needs to be modified to accommodate the results of this study.

The current management regime relies on catch and stock size projections based on an $F_{0.1}$ strategy. The use of a reference point such as $F_{0.1}$ is probably not very useful for mackerel since growth, sexual maturity, and natural mortality rates appear to fluctuate considerably. This concept is best applied in situations where these important variables are stable in the long term. A more appropriate approach might be to remove a moderately large sustainable catch annually or apply an appropriate constant effort level over several years, preserve a reasonable amount of spawning-stock biomass, and monitor the results. This method would be keyed to some of the uncertainties in stock dynamics that we have investigated in this study and would provide information on stock responses with a low probability of stock collapse (i.e., F = 0.2–0.3; Fig. 11C).

Additional analyses are necessary to confirm the population processes that were modeled in this study. Weights of individual fish should be monitored closely to assess future changes. Sexual maturities of ages 2–3 fish should also be followed annually. Collection of these data would also allow better parameterization of the growth and maturity models. Sufficient samples must be collected at the correct times to assess whether these two variables, particularly percent maturity, are continuing to change with stock density. Additional food habits sampling at critical times and places would help confirm and quantify the relationships found in this analysis. Obtaining some information on predation mortality on age-0 mackerel would be valuable.

Preliminary data suggest that predator preference may play an important role in determining the levels of predation on available prey species. Recent declines in sand lance *Ammodytes dubius* populations may increase predation mortality on mackerel and Atlantic herring *Clupea harengus*. This points to the need for a multispecies VPA where simultaneous impacts of predation may be investigated. Improved predation models that account for predator preference and prey abundance would allow for more accurate predictions of the impacts of these important factors, and better management advice could be provided (Livingston 1986). Larger mackerel are preyed upon by marine mammals, large pelagic fishes, and sea birds (Stillwell and Kohler 1982, 1985; Payne and Selzer 1983; Payne et al. 1984; Overholtz et al. 1990). The impact of these predators is no doubt important, but was not evaluated in this study.

Acknowledgments

We thank the personnel from the Northeast Fisheries Center and other institutions who have collected data on research surveys over the last 25 years. We are grateful to the foreign fishery observers and scientists who collected data from the Polish commercial fishery. Special thanks to Louise Dery who provided the age data for the study. We would also like to thank Brian Rothschild for his guidance and insight in the initial phases of this research.

Citations

Anderson, E.D.
1985 Status of the Northwest Atlantic mackeral stock—1984. Ref. Doc. 85-03, Woods Hole Lab., Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA, 46 p.

Anderson, K.P., and E. Ursin
1977 A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorous circulation and primary production. Medd. Dan. Fisk. Havunders. 7:319–435.

Anderson, R.M.
1979 The influence of parasitic infection on the dynamics of host population growth. *In* Anderson, R.M., B.D. Turner, and L.R. Taylor (eds.), Population dynamics, p. 245-281. Blackwell Sci. Publ., Oxford.

Bowman, R.E., and W.L. Michaels
1984 Food of seventeen species of northwest Atlantic fish. NOAA Tech. Memo. NMFS-F/NEC-28, Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA, 183 p.

Bowman, R.E., R. Eppi, and M.D. Grosslein
1984 Diet and consumption of spiny dogfish in the northwest Atlantic. ICES Demersal Fish Comm., ICES CM 1984/G:27, 16 p.

Holling, C.S.
1965 The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 91:293–320.

Hoy, D.L., and G.M. Clark
1967 Atlantic mackerel fishery, 1804–1965. Fish. Leafl. 603, U.S. Dep. Inter., Wash. DC, 9 p.

ICES (International Council for the Exploration of the Sea)
1987 Report of the ad hoc multispecies assessment working group. ICES CM 1987/Assess:9, 130 p.
1988 Report of the multispecies assessment working group. ICES CM 1988/Assess:23, 154 p.

Jenson, A.C.
1967 A brief history of the New England offshore fisheries. Fish. Leafl. 594, U.S. Dep. Inter., Wash. DC, 14 p.

Langton, R.W., and R.E. Bowman
1980 Food of fifteen northwest Atlantic gadiform fishes. NOAA Tech. Rep. NMFS SSRF 740, 23 p.

Lett, P.F.
1980 A comparative study of the recruitment mechanisms of cod and mackerel, their interaction, and its implication for dual stock assessment. Can. Tech. Rep. Fish. Aquat. Sci. 988, 45 p.

Livingston, P.A.
1986 Incorporating fish food habits data into fish population assessment models. *In* Simenstad, C.A., and G.M. Cailliet (eds.), Contemporary studies on fish feeding, p. 225-234. Dr. Junk Publ., Dordrecht, Netherlands.

McKay, K.T.
1979 Synopsis of biological data of the northern population of Atlantic mackerel (*Scomber scombrus*). Can. Fish. Mar. Serv. Tech. Rep. 885, 26 p.

Murdoch, W.W.
1973 The functional response of predators. J. Appl. Ecol. 10: 335–342.

NEFC (Northeast Fisheries Center)
1987 Report of the fourth NEFC stock assessment workshop. Ref. Doc. 87-07, Woods Hole Lab., Northeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA, 102 p.

Overholtz, W.J.
1989 Density dependent growth in the northwest Atlantic stock of Atlantic mackerel. J. Northwest Atl. Fish. Sci. 9:127–135.

Overholtz, W.J., and B.L. Parry
1985 Update of the status of the northwest Atlantic mackerel stock for 1985. Ref. Doc. 85-113, Woods Hole Lab., Northeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA, 5 p.

Overholtz, W.J., and A.V. Tyler
1986 An exploratory simulation model of competition and predation in a demersal fish assemblage on Georges Bank. Trans. Am. Fish. Soc. 115:805–817.

Overholtz, W.J., S.A. Murawski, W.L. Michaels, and L.M. Dery
1988 The effects of density dependent population mechanisms on assessment advice for the northwest Atlantic mackerel stock. NOAA Tech. Memo. NMFS F/NEC-62, Northeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA, 49 p.

Overholtz, W.J., S.A. Murawski, and K.L. Foster
In press Impact of predatory fish, marine mammals, and seabirds on the pelagic fish ecosystem of the Northeastern USA. *In* Daan, N., and M. Sissenwine (eds.), Symposium on multispecies models relevant to management of living resources, The Hague, Netherlands, October 1989. Rapp. P.-V. Reun. Cons. Int. Explor. Mer.

Payne, P.M., and L.A. Selzer
1983 Population distribution, abundance, and prey requirements of the harbor seal in southern New England. NMFS Contract Rep. NA-82-FA-00007, by Manomet Bird Observatory, Manomet, MA. Northeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA, 51 p.

Payne, P.M., L.A. Selzer, and A.R. Knowlton
1984 Distribution and density of cetaceans, marine turtles, and seabirds in the shelf waters of the northeastern United States, June 1980–December 1983, based on shipboard observations. NMFS Contract Rep. NA-81-FA-C-00023, by Manomet Bird Observatory, Manomet, MA. Northeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA, 246 p.

Pope, J.G.
1976 The effect of biological interactions on the theory of mixed fisheries. Int. Comm. Northwest Atl. Fish. Sel. Pap. 1:163–170.
1979 A modified cohort analysis in which constant natural mortality is replaced by estimates of predation levels. ICES Pelagic Fish Comm., ICES CM 1979/H:16, 15 p.

Rexstad, E.A., and E.K. Pikitch
1986 Stomach contents and food consumption estimates of Pacific hake, *Merluccius productus*. Fish. Bull., U.S. 84: 947–956.

Sette, O.E.
1950 Biology of the Atlantic mackerel (*Scomber scombrus*) of North America: Part 2: Migrations and habits. Fish. Bull., U.S. 51:251–358.

Sette, O.E., and W.H. Needler
1934 Statistics of the mackerel fishery off the coast of North America. Invest. Rep. 19, U.S. Dep. Commer., Wash. DC, 48 p.

Shepherd, J.G.
1982 A versatile new stock-recruitment relationship for fisheries and the construction of sustainable yield curves. J. Cons. Cons. Int. Explor. Mer 40:67–75.
1984 A promising method for the assessment of multispecies fisheries. ICES Demersal Fish Comm., ICES CM 1984/G:4, 12 p.

Sherman, K., C. Jones, L. Sullivan, W. Smith, P. Berrien, and L. Ejsymont
1981 Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. Nature (Lond.) 291: 486–489.

Sissenwine, M.P.
1977 A compartmentalized simulation model of the Southern New England yellowtail flounder, *Limanda ferruginea*, fishery. Fish. Bull., U.S. 75:465–482.

Sparre, P.
1984 A computer program for estimation of food suitability coefficients from stomach content data and multispecies VPA. ICES Demersal Fish Comm., ICES CM 1984/G:25, 60 p.

Stillwell, C.E., and N.E. Kohler
1982 Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 39:407–414.
1985 Food and feeding ecology of the swordfish *Xiphias gladius* in the western north Atlantic ocean with estimates of daily ration. Mar. Ecol. Prog. Ser. 22:239–247.

Walters, C.J.
1969 A generalized computer simulation model for fish population studies. Trans. Am. Fish. Soc. 98:505–512.

Walters, C.J., M. Stocker, A.V. Tyler, and S.J. Westrheim
1986 Interaction between Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus pallasi*) in the Hecate Strait, British Columbia. Can. J. Fish. Aquat. Sci. 43:830–837.

Abstract.–The equilibrium contribution of hatchery-released juveniles to a rockfish fishery is evaluated by using a yield-per-recruit model. Hatchery-released juveniles may be worth up to an estimated US$0.16 per juvenile to the fishery. The use of hatchery releases to restore a depleted population of Pacific ocean perch *Sebastes alutus* is examined with the Deriso-Schnute model. This model indicates that hatchery releases have the potential to substantially increase a stock's yield and rate of recovery during the recovery period.

Evaluation of Hatchery Releases of Juveniles to Enhance Rockfish Stocks, with Application to Pacific Ocean Perch *Sebastes alutus**

Jeffrey J. Polovina

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
2570 Dole Street, Honolulu, Hawaii 96822-2396

There is a long history of attempts worldwide to enhance marine fisheries by releasing hatchery-reared juveniles. However, few attempts have had long-term success (Yatsuyanagi 1982, Botsford and Hobbs 1984, Isibasi 1984, Ulltang 1984). In theory, hatchery releases can enhance fisheries in two ways. First, juvenile releases can be added to the natural stock on a long-term basis to support a higher level of fishery harvest than that achieved from the natural stock alone. Secondly, juvenile releases can be used on a short-term basis to increase a depleted natural stock more rapidly, then discontinued once the natural stock has recovered.

Pilot releases of the rockfish *Sebastes schlegeli* indicate that large-scale rearing and releases of rockfish may be biologically and technically possible (Sakai et al. 1985, Kusakari In press). The merit of hatchery releases of juveniles for fishery enhancement is examined in the present paper with mathematical models. Specifically, the Beverton and Holt (1966) yield-per-recruit model will be used to evaluate the sustainable increase in fishery catches from a long-term release of hatchery-reared juveniles. The Deriso-Schnute delay-difference age-structure model (Zheng and Walters 1988) will be used to evaluate the fishery benefits from short-term juvenile releases to increase the recovery of depleted rockfish stocks.

Models and methods

To evaluate the equilibrium contribution of hatchery-released juveniles to a rockfish fishery, the Beverton and Holt (1966) equation was used to express the equilibrium yield-per-recruit as a function of the following ratios: instantaneous natural mortality to von Bertalanffy growth (M/K), length at recruitment to asymptotic length, and fishing mortality to natural mortality (F/M) (Beverton and Holt 1966). If a recruit in the yield-per-recruit model is taken to represent a hatchery-released juvenile rather than a recruit from the natural population, then the equilibrium yield per hatchery-released juvenile can be computed from yield-per-recruit tables (Beverton and Holt 1966). Specifically, let Y/R_0 denote the yield per recruit where the recruits are of some reference age, say the age at which they have just become demersal. Then the yield per released fish at age t is just

$$\frac{Y}{R_0} e^{Mt}$$

where M is the natural mortality rate from the reference age 0 until release age t. The values of Y/R_0 are tabled as a function of M/K and F/M (Beverton and Holt 1966). The equilibrium yield per hatchery-released juvenile

*Presented at U.S.–Japan Symposium on Reproduction and Early Life History in the Genus *Sebastes*, Honolulu, Hawaii, June 1989.

Manuscript accepted 7 August 1990.
Fishery Bulletin, U.S. 89:129–136 (1991).

Table 1

Von Bertalanffy growth (K), natural mortality (M), M/K, and maximum age for seven commercially important species of rockfish (parameter estimates taken from Pacific Fishery Management Council 1989).

Common name	M/yr	K/yr	M/K	Max. age (yr)
Pacific ocean perch	0.05	0.09	0.56	70+
Yellowtail	0.07	0.16	0.44	64
Shortbelly	0.25	0.21	1.19	12
Widow	0.15–0.20	0.15	1.17*	58
Canary	0.01–0.09	0.16	0.31*	75
Chilipepper	0.20	0.18	1.11	16
Bocaccio	0.25	0.11	2.27	36

*M taken as the midpoint of the range.

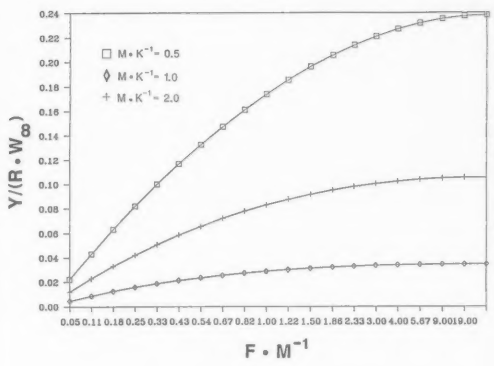


Figure 1

Beverton and Holt yield-per-recruit as a fraction of asymptotic weight at optimum size at entry to the fishery as a function of F/M for three levels of M/K.

will be estimated for values of release age t, M, M/K, and F/M, which are representative estimates for rockfish populations.

To evaluate the short-term releases of hatchery-reared juveniles to restore a depleted rockfish population, a Deriso-Schnute delay-difference age-structure model is used (Zheng and Walters 1988). Deriso (1980) derived a population model that combined simple surplus production models with more detailed age-structure models. Schnute (1985) modified this model with a three-parameter Brody growth model. This Deriso-Schnute model depends on a Brody growth parameter (p), the age of recruitment to a fishery (k), body weights at ages k and $k-1$ (W_k and W_{k-1}, respectively), and total annual survival in year t (s_t). Thus, the biomass in year $t+1$ (B_t+1) is described as

$$B_{t+1} = (1+p)s_tB_t - ps_ts_{t-1}B_{t-1} + R_{t+1} - ps_t\frac{W_{k-1}}{W_k}R_t,$$

where R_t is the recruitment to the fishery in year t (Schnute 1985). A Ricker stock-recruitment relationship is used to model the recruitment (in weight) from the natural rockfish population and from hatchery-released 1-year-old juveniles to the fishery to obtain the total recruitment (in weight) function (R_t):

$$R_t = AS_{t-k}\exp(-BS_{t-k})\exp(z) + H_{t-k+1}W_k\exp(-M(k-1));$$

where S_t is the spawning biomass, H_t is the number of hatchery-released 1-year-old juveniles, M is natural mortality, and A and B are constants. This model assumes hatchery juveniles are added to the natural population without any density-dependence. The term exp(z) is used to add a stochastic element to the natural recruitment function when the variable z represents a random variable, which has a normal distribution, a mean of 0, and a variance of σ^2. When σ^2 is set to 0, the stochastic term is eliminated, and deterministic recruitment is assumed. The Ricker stock-recruitment relationship appears to represent an appropriate model of recruitment in a natural rockfish population (Archibald et al. 1983).

The Deriso-Schnute model is fit to catch and fishing mortality data for Pacific ocean perch *Sebastes alutus* from Queen Charlotte Sound, Canada, during 1963–77 when the population was fished from an estimated biomass of 82,000 metric tons (t) to 13,000 t (Archibald et al. 1983). The model with its estimated parameters is then used to estimate the equilibrium yield curve to determine the biomass and fishing mortality that achieve maximum sustainable yield (MSY). Then the model with stochastic recruitment is used to simulate the recovery of this depleted stock to the biomass level that supports MSY under several management strategies, including the release of hatchery-reared juveniles.

Results

Values of M for rockfishes typically range from 0.01 to 0.25 per year, K from 0.09 to 0.21 per year, and M/K ratios from 0.44 to 2.27 (Table 1). Values of yield-

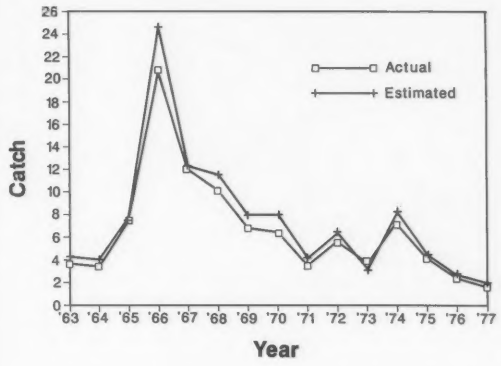


Figure 2
Historic catches (10^3 metric tons) of Pacific ocean perch from Queen Charlotte Sound and estimated catches from the fit of the Deriso-Schnute model, 1963–77.

Table 2
Parameters for the Deriso-Schnute model fit to Pacific ocean perch in Queen Charlotte Sound.

Parameter	Value	Source
Recruitment age (k)	9 years	Archibald et al. (1983)
Natural mortality (m)	0.05 per year	Archibald et al. (1983)
Weight at entry (W_k)	0.614 kg	Archibald et al. (1983)
Weight at age $k-1$ (W_{k-1})	0.572 kg	Archibald et al. (1983)
Body growth (p)	0.52 per year	Estimated as mean of range: $1-\sqrt{\frac{W_k}{W_\infty}} \leq p \leq 1-\frac{W_k}{W_\infty}$
Recruitment model	Ricker	Archibald et al. (1983)
Recruitment parameters A, B	A = 0.29 $B = 1.6\times10^{-5}$	From fit of model to 1963–77 data

per-recruit (expressed as a fraction of the asymptotic weight of the fish, as a function of F/M, and for M/K equaling 0.5, 1.0, and 2.0) are shown in Figure 1. These yield curves assume that the ratio of the length-at-recruitment to the asymptotic length is optimum to achieve maximum yield-per-recruit. For M/K ranging from 0.5 to 2.0, the optimum length at harvest will be 45–86% of the asymptotic length (Beverton and Holt 1966). Thus, in the case of Pacific ocean perch, which has an asymptotic weight of about 1.4 kg, if M/K = 0.5, F/M = 1.0, and M = 0.05 per year, the contribution to the fishery of an individual juvenile released from the hatchery at age 0.25 is calculated as the product of 1.4 kg × 0.17 (from Fig. 1), multiplied by exp(0.05 · 0.25) or 0.24 kg. The average 1988 ex-vessel price for all rockfishes was US$0.67 per kg (National Marine Fisheries Service 1989); therefore, each 3-month-old, hatchery-released juvenile on the average is worth $0.16 to the fishery. The contribution of a juvenile to the fishery is strongly inversely related to M/K (Fig. 1). For example, if M/K is 1.0 rather than 0.5, then the contribution is only about one-half as much. Also, as long as natural mortality is assumed to be low and constant, changes in the release age have little influence on the contribution of the juvenile to the fishery. However, it is quite possible that natural mortality of young juveniles varies considerably by age and an optimum release age exists, although we have no data to document either case.

Pacific ocean perch in Queen Charlotte Sound, Canada, underwent heavy exploitation from 1963 to 1977 (Fig. 2) (Archibald et al. 1983). A reconstruction of the history of this exploitation by using a catch-at-age model estimates annual exploitable biomass and average fishing mortality during this period (Archibald et al. 1983). The Deriso-Schnute model is fit to the catch history of this fishery during 1963–77 by using estimates of fishing mortality from the catch-at-age model (Fig. 2). All but two of the parameters required for the model are from published values (Table 2). Two parameters (A and B in Table 2) in the stock-recruitment relationship part of the model are estimated by fitting the model to the 1963–77 catch series.

Based on the Deriso-Schnute delay-difference model with the parameters used to fit the catch and effort series (1963–77) and to estimate the equilibrium yield curve, the maximum sustainable yield (MSY) of about 1800 t is achieved at F_{MSY} = 0.06 per year (Fig. 3). At that level of F_{MSY}, the corresponding equilibrium biomass (B_{MSY}) is estimated at about 35,000 t. At B_{MSY}, the recruitment of 1-year-old juveniles is estimated at 3.5 million fish, whereas an estimated 1.3 million 1-year-olds recruit if biomass is at the 1977 depleted levels.

Assuming that the goal of restoring the Pacific ocean perch stock is to increase the biomass to 35,000 t so it can be harvested at F = 0.06 to achieve MSY, three approaches to stock recovery are examined. One approach has as its goal to increase the biomass to B_{MSY} as quickly as possible by setting F at 0 until the biomass reaches 35,000 t, then the stock will be fished at

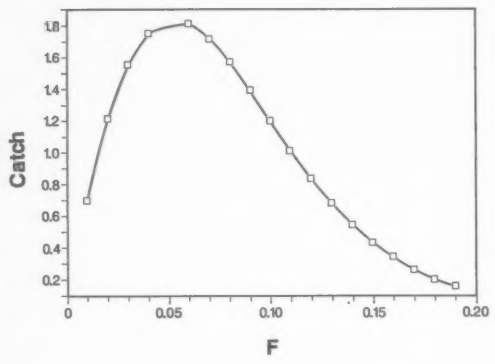


Figure 3
Equilibrium yield curve (10^3 metric tons) for Pacific ocean perch from Queen Charlotte Sound estimated from the Deriso-Schnute model.

F = 0.06. The second approach to stock recovery is to eventually achieve B_{MSY} while also maximizing the yield to the fishery. Under this approach, the stock is fished at F = 0.06 from the beginning. A third strategy, which represents a compromise between these two philosophies, will set F at 0.03 until the biomass reaches 35,000 t, then the stock will be fished at F = 0.06.

Each of these three sequences of F can be evaluated with and without hatchery releases. Catch and biomass series with and without hatchery releases for each sequence of F can be simulated with the stochastic Deriso-Schnute model with the parameters used to fit the population decline. When hatchery releases are used, 5 million 1-year-old juveniles will be stocked annually. This number represents almost four times the natural recruitment for the stock at the 1977 depleted level and about 40% more than the natural recruitment at the B_{MSY} level. The variance of the random variable z in the stochastic recruitment component is assumed to have a variance of 0.3 (Archibald et al. 1983). Based on 100 simulations of each of the six management approaches over 100 years, the mean annual catches, mean cumulative catches and the biomass distributions after 20 years can be computed (Figs. 4–6, Table 3).

When the management strategy closes the stock to fishing to restore it as quickly as possible, B_{MSY} (35,000 t) is achieved in 21 years without stocking and 14 years if 5 million juveniles are stocked annually for 6 years (Table 3). After 20 years, the mean biomass levels are about the same for the stocked and non-stocked cases, so annual catches are about the same and the difference in cumulative yield remains con-

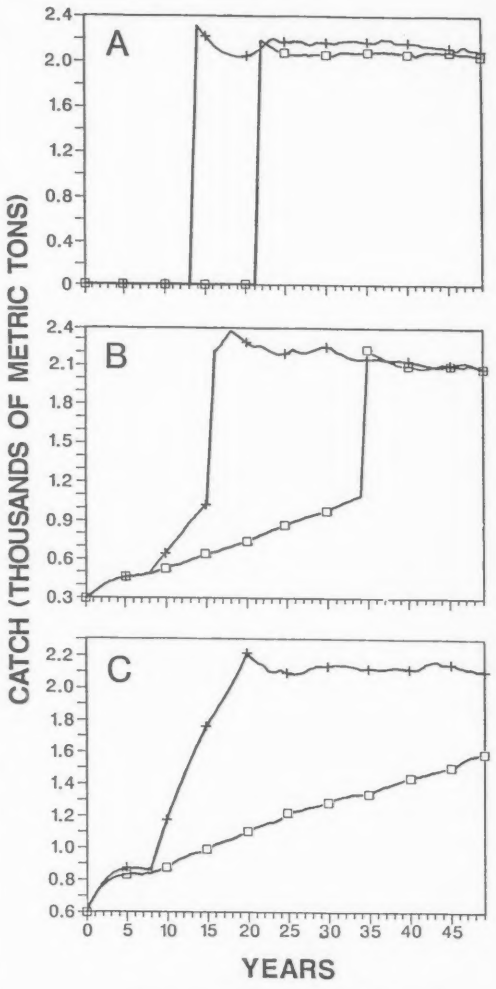

CATCH (THOUSANDS OF METRIC TONS)
A
B
C
YEARS
A F = 0, years 1-21; F = 0.06, years 22-50 (□—□)
F = 0, years 1-14; F = 0.06, years 15-50, with stocking of 5 million per year for 6 years (+—+)
B F = 0.03, years 1-35; F = 0.06, years 36-50 (□—□)
F = 0.03, years 1-16; F = 0.06, years 17-50, with stocking of 5 million per year for 10 years (+—+)
C F = 0.06, years 1-50 (□—□)
F = 0.06, years 1-50, with stocking of 5 million per year for 12 years (+—+)

Figure 4
Simulated annual catches of Pacific ocean perch, with and without hatchery releases, for three management strategies.

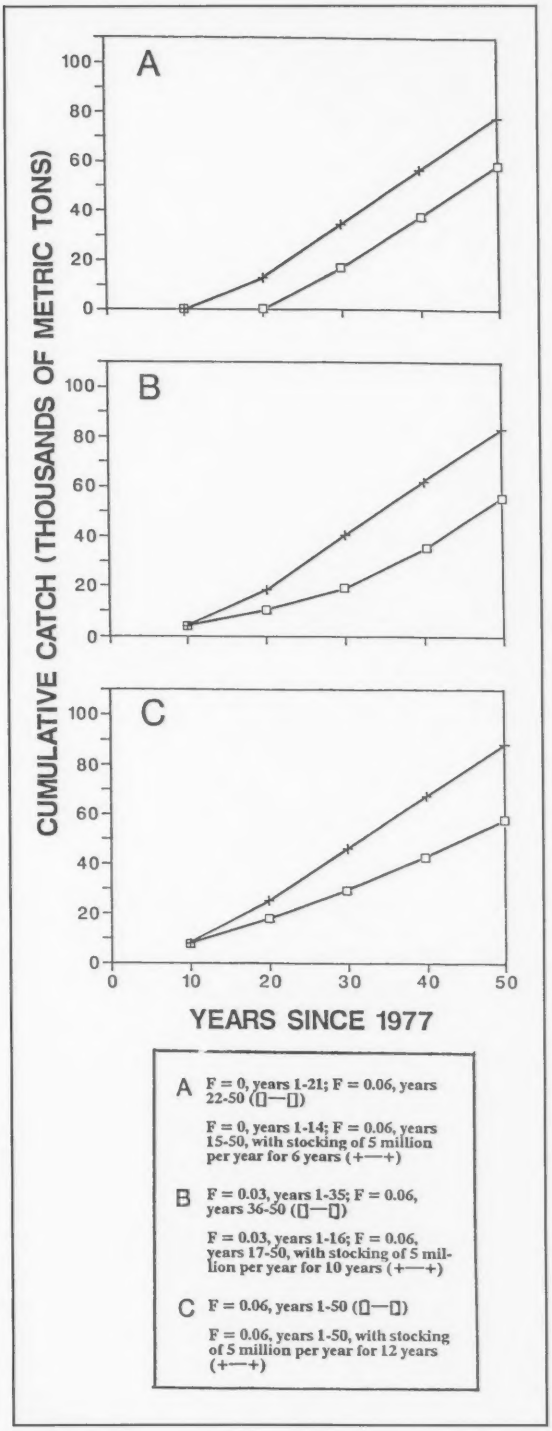

A
B
C
CUMULATIVE CATCH (THOUSANDS OF METRIC TONS)
YEARS SINCE 1977
A F = 0, years 1-21; F = 0.06, years 22-50 (□—□)
F = 0, years 1-14; F = 0.06, years 15-50, with stocking of 5 million per year for 6 years (+—+)
B F = 0.03, years 1-35; F = 0.06, years 36-50 (□—□)
F = 0.03, years 1-16; F = 0.06, years 17-50, with stocking of 5 million per year for 10 years (+—+)
C F = 0.06, years 1-50 (□—□)
F = 0.06, years 1-50, with stocking of 5 million per year for 12 years (+—+)

Figure 5
Simulated cumulative catches of Pacific ocean perch, with and without hatchery releases, for three management strategies.

stant (Figs. 4,5). The biomass distributions with and without stocking are very similar after 20 years (Fig. 6).

When F = 0.03, B_{MSY} is achieved in 35 years without stocking and in 17 years when 5 million juveniles are stocked annually for 10 years (Table 3). The annual catches for both the stocked and nonstocked strategies are the same for the first 8 years because of the 8-year lag between the release of juveniles and their entry into the fishery; but beginning in year 9, the annual catches in the stocked strategy exceed those for the nonstocked strategy. In year 16, B_{MSY} is achieved in the stocked strategy, and F is increased to 0.06, which results in a substantial increase in annual catches. The annual catches for the nonstocked strategy lag behind the stocked catches until year 35 when B_{MSY} is achieved and F is increased to 0.06 (Fig. 4). The difference between the cumulative catches for stocked and nonstocked is initially very small, because the two strategies have the same annual catches at the beginning, but the difference grows once the annual catches diverge (Fig. 5). After 20 years, the distribution of biomass for the stocked population is about 10,000 t greater than for the population without stocking (Fig. 6).

When F = 0.06, B_{MSY} is not achieved within 100 years without stocking, whereas B_{MSY} is achieved in 20 years with stocking (Table 3). The patterns of annual and cumulative catches for the stocked and nonstocked cases are similar to the F = 0.03 situation (Figs. 4,5). After 20 years, the distribution of biomass without stocking shows very little change from the level at the beginning of the recovery period, whereas the distribution of the stocked population centers close to B_{MSY} (Fig. 6).

The value of stocking to increase yields while restoring the depleted Pacific ocean perch population can be evaluated by computing the break-even cost of a hatchery-released juvenile based on the increase in cumulative landings. Suppose a hatchery, built and operated by government funds, must meet the economic criterion of a 3% return on investment. Then the break-even cost per juvenile, as a function of n years after the start of stocking, can be calculated as follows: (1) Compute the increase in cumulative yield between the comparable stocked and nonstocked strategies, n years

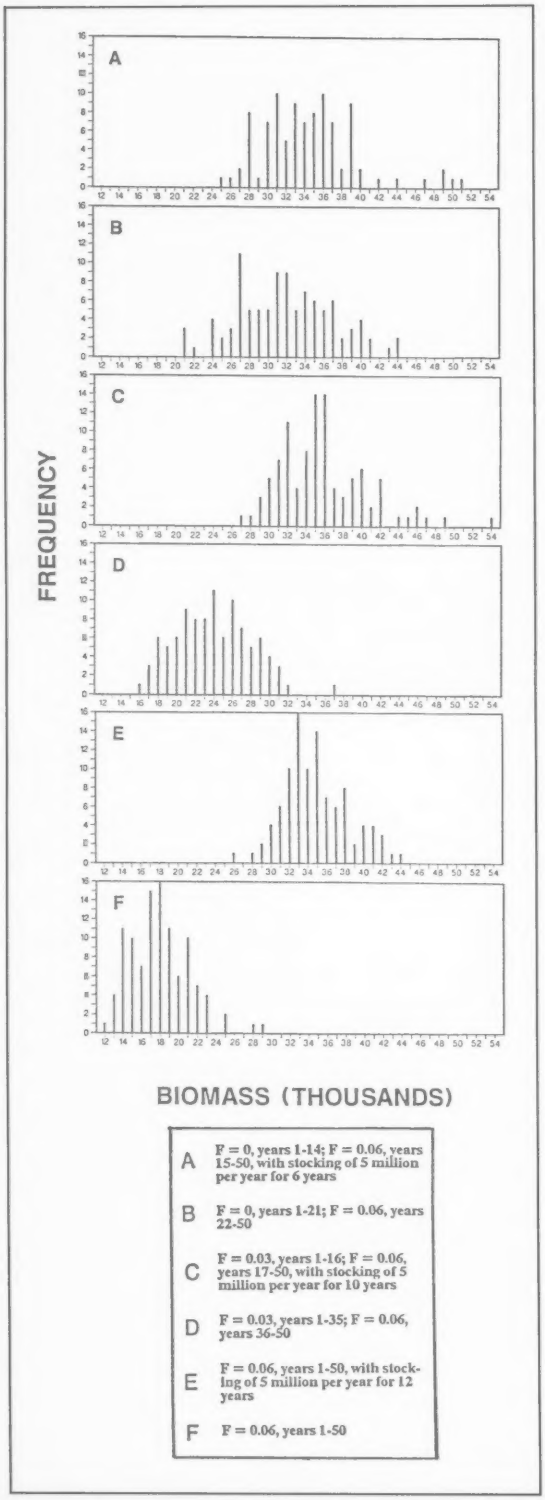

A
B
C
D
E
F
FREQUENCY
BIOMASS (THOUSANDS)
A F = 0, years 1-14; F = 0.06, years 15-50, with stocking of 5 million per year for 6 years
B F = 0, years 1-21; F = 0.06, years 22-50
C F = 0.03, years 1-16; F = 0.06, years 17-50, with stocking of 5 million per year for 10 years
D F = 0.03, years 1-35; F = 0.06, years 36-50
E F = 0.06, years 1-50, with stocking of 5 million per year for 12 years
F F = 0.06, years 1-50

Figure 6
Biomass distributions of Pacific ocean perch 20 years after the onset of hatchery releases (from 100 simulations), with and without stocking, for three management strategies.

after the start of stocking; (2) divide this increase in yield (the result from step 1) by the total number of juveniles stocked to obtain the increase in yield per stocked juvenile; (3) multiply the result of step 2 by the unit value of the yield to the fishery to compute the value to the fishery per stocked juvenile; and, finally, (4) discount this yield cumulated over n years to a present value by dividing the result of step 3 by $(1.03)^n$. Using this approach, based on a wholesale value for Pacific ocean perch of \$0.67 per kg (National Marine Fisheries Service 1989), the break-even cost per juvenile ranges from \$0.04 to \$0.16. For example, under the scenario where the fishery is closed until B_{MSY} is reached, if hatchery juveniles can be stocked at a cost of \$0.16 per juvenile, then hatchery releases result in increasing the value of the catches over the nonstocked strategy equivalent to a 3% annual return on stocking costs for the first 20 years after stocking (Table 4). However, under the scenario where F = 0.06 from the beginning of the recovery period, the break-even cost of a hatchery-released juvenile cannot exceed \$0.04 if the release program is to achieve a 3% annual return over the first 10 years and \$0.08 over a 40-year period.

Looking at just the cumulative yields does not show all of the benefits of stocking, since some of the released juveniles contribute to an increase in standing stock. When the contribution of the released juveniles to both the fishery and standing stock is considered, the relative benefit is the same for all three stocking and harvesting strategies (Table 5).

A delay-difference model very similar to the model used in this analysis, but with a Cushing rather than Ricker recruitment function, has been fit to data on the Pacific ocean perch fishery in waters off Washington and Oregon (Ito et al. 1987). When the Cushing recruitment function is used in our model, the estimates of MSY, F_{MSY} and B_{MSY} change, but the relative contribution of hatchery releases to biomass and yield is unchanged (Table 5). Further, based on simple sensitivity analyses, the relative benefits of hatchery releases by increasing biomass and yield apparently are most sensitive to the ratio of natural mortality to growth (Table 5). Thus, as in the yield-per-recruit model, the relative benefits of hatchery releases are inversely proportional to the ratio of mortality to growth.

Table 3

Catch of Pacific ocean perch cumulated by 10-year periods from the mean of 100 simulations of the Deriso-Schnute model (thousands of metric tons).

Strategy	Years to B_{MSY} (N)	No. of years for which catch is cumulated 10	20	30	40	50
F = 0, years 1–21; F = 0.06, years 11–50	21	0	0	16.8	37.7	58.6
F = 0, years 1–14; F = 0.06, years 15–50, with stocking of 5 million/year for 6 years	14	0	13.0	34.5	56.5	77.9
F = 0.3, years 1–35; F = 0.06, years 36–50	35	4.4	10.6	19.2	35.2	56.2
F = 0.03, years 1–16; F = 0.06, years 17–50, with stocking of 5 million/year for 10 years	16	4.5	18.5	39.7	61.2	82.3
F = 0.06, years 1–50	100+	8.0	17.8	29.8	43.3	58.3
F = 0.06, years 1–50, with stocking of 5 million for 12 years	20	8.3	25.1	46.3	67.5	88.9

Table 4

Break-even cost of hatchery-released juveniles of Pacific ocean perch at a 3% annual rate of return (US$ per juvenile) as a function of years after start of releases.

Strategy	Years 10	20	30	40	50
F = 0, years 1–21; F = 0.06, years 22–50 **versus** F = 0, years 1–14; F = 0.06, years 15–20, with stocking of 5 million/year for 6 years	0	0.16	0.16	0.12	0.09
F = 0.03, years 1–35; F = 0.06, years 36–50 **versus** F = 0.03, years 1–16; F = 0.06, years 17–50, with stocking of 5 million/year for 10 years	0	0.06	0.11	0.11	0.08
F = 0.06, years 1–50 **versus** F = 0.06, years 1–50, with stocking of 5 million/year for 12 years	0	0.04	0.07	0.08	0.07

Table 5

Contribution of juvenile releases of Pacific ocean perch to biomass and cumulative yield 20 years after the start of releases.

Strategy	I Change in biomass per released juvenile (kg/fish)	II Change in yield per released juvenile (kg/fish)	II + III (kg/fish)
A	0	0.43	0.43
B	0.25	0.16	0.41
C	0.31	0.11	0.42
D	0.33	0.08	0.41
E	0.28	0.14	0.42
F	0.18	0.05	0.23
G	0.22	0.26	0.48
H	0.33	0.14	0.47

A: F = 0, years 1–21; F = 0.06, years 22–50 vs. F = 0, years 1–14; F = 0.06, years 15–50, with 5 million juvenile releases for 6 years.
B: F = 0.03, years 1–35; F = 0.06, years 36–50 vs. F = 0.03, years 17–50, with 5 million juvenile releases for 10 years.
C: F = 0.06 vs. F = 0.06, with 5 million juvenile releases for 12 years.
D: F = 0.04 vs. F = 0.04, with 5 million juvenile releases for 12 years.
E: F = 0.08 vs. F = 0.08, with 5 million juvenile releases for 12 years.
F: M = 0.1 instead of M = 0.05 and strategy C.
G: F = 0.08 vs. F = 0.08, with 5 million juvenile releases for 3 years with growth, mortality, and Cushing recruitment model (parameter estimates are from Ito et al. 1987).
H: F = 0.04 vs. F = 0.04, with 5 million juvenile releases for 5 years with growth, mortality, and Cushing recruitment model (parameter estimates are from Ito et al. 1987).

Discussion

The Beverton and Holt (1966) model provides a simple means of evaluating the equilibrium contribution of a long-term hatchery release program to the fishery. The model shows that if M/K is 0.5 for the hatchery-released juveniles from the time of release to capture in the fishery, and if the cost of each released juvenile is less than US$0.16, its value to the fishery exceeds its cost. The length-at-entry for fish in these analyses is assumed to be the length that maximizes the yield-per-recruit, that is, 45–86% of the asymptotic length. If the length-at-entry to the fishery is below this level, as with some long-lived, slow-growing fishes, the contribution of the hatchery releases to the fishery will be less than the value calculated by the model. However, the yield-per-recruit surface is relatively flat, so unless the length-at-entry is widely different from the optimum length, the reduction in the contribution of the hatchery releases should not exceed 10–15% of the

value corresponding to the optimum length-at-entry (Beverton and Holt 1966). The results of the model are particularly sensitive to levels of M/K, asymptotic weight, and market price. Interestingly, the results depend only on the ratio of M to K, and the slow growth of rockfish does not have a bearing on the equilibrium benefit of the released juveniles. Three commercially important species—Pacific ocean perch, yellowtail rockfish *Sebastes flavidus*, and canary rockfish *S. pinniger*—have M/K values around 0.5 and, from a population dynamics standpoint, offer the most potential for hatchery releases (Table 1).

Based on the Deriso-Schnute model, the level of F_{MSY} for Pacific ocean perch in Queen Charlotte Sound is estimated at 0.06 per year. This value is consistent with the finding of Archibald et al. (1983) and considerably less than the F levels of 0.2–0.5 per year during the depletion of the stock. Given the slow growth and long lag between spawning and recruitment to the fishery, stock recovery for rockfish is a long-term process. Fishery managers must decide whether the goal of the recovery program is to return the stock to B_{MSY} as quickly as possible or to follow a more gradual return while allowing fishing. Under both approaches, stocking reduces the time to reach B_{MSY} and increases the yield to the fishery. Both benefits must be considered in evaluating the merits of a hatchery-release program for stock recovery. As with the yield-per-recruit analysis, Pacific ocean perch, yellowtail rockfish, and canary rockfish are the three commercial species, based on their low M/K ratios, that offer the most potential for stock recovery with hatchery releases (Table 1).

Based on population-dynamics considerations, the use of hatchery releases for fishery enhancement appears to have merit for certain species of rockfishes. However, population dynamics represents only one part of the post-release ecology, and a fuller understanding of this ecology is necessary to predict the success of hatchery releases. For example, hatchery-reared Kuruma prawns *Penaeus japonicus* were released in a number of similar locations around Japan (Isibasi 1984). Increases in catches were documented in some instances, but no changes were evident in many others; researchers generally were unable to explain this variation (Isibasi 1984). While this analysis assumes that large-scale hatchery releases are possible, no such releases have been done, and nothing is known of the economics of a rockfish hatchery. Further, hatchery-released juveniles have been assumed to have the same behavior and natural mortality as wild stock. This may be an overly optimistic assumption because pilot hatchery releases for other species often have higher and more variable natural mortality than is thought to occur in wild stock (Kyokai 1983).

Citations

Archibald, C.P., D. Fournier, and B.M. Leaman
1983 Reconstruction of stock history and development of rehabilitation strategies for Pacific ocean perch in Queen Charlotte Sound, Canada. N. Am. J. Fish. Manage. 3:283–294.

Beverton, R.J.H., and S.J. Holt
1966 Manual of methods for fish stock assessment. Part II - Tables of yield functions. FAO Fish. Tech. Pap. 38 (Rev. 1), 67 p.

Botsford, L.W., and R.C. Hobbs
1984 Optimal fishery policy with artificial enhancement through stocking: California's white sturgeon as an example. Ecol. Modell. 23:293–312.

Deriso, R.B.
1980 Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. 37:268–282.

Isibasi, K.
1984 A statistical assessment on the effect of liberation of larvae in the sea farming—I. On the effect of liberation in the case of Kuruma prawn (*Penaeus japonicus*). Bull. Tokai Reg. Fish. Res. Lab. 113:141–155.

Ito, D.H., D.K. Kimura, and M.E. Wilkins
1987 Status and future prospects for the Pacific ocean perch resource in waters off Washington and Oregon as assessed in 1986. NOAA Tech. Memo. NMFS-F/NWC-113, Northwest & Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle 98115, 50 p.

Kusakari, M.
In press Mariculture of kurosoi, *Sebastes schlegeli*. Environ. Biol. Fish.

Kyokai, S. (editor)
1983 Tsukuru gyogyo. Norin Tokei Kyokai (Agric. For. Stat. Assoc.), 753 p. [in Jpn., Engl. transl. of Table of Contents only by T. Otsu, 1987; full translation avail. from JJP].

National Marine Fisheries Service
1989 Fisheries of the United States, 1988. U.S. Natl. Mar. Fish. Serv. Curr. Fish. Stat. 8800, 116 p.

Pacific Fishery Management Council
1989 Pacific coast groundfish fishery management plan, draft amendment 4. Pac. Fish. Manage. Counc., Portland, OR, 52 p.

Sakai, K., H. Nagashima, and K. Kiso
1985 Growth and movement of artificially reared young rockfish, *Sebastes schlegeli*, after release in Matsushima Bay. Bull. Tohoku Reg. Fish. Res. Lab. 47:21–32 [in Jpn., Engl. abstr; Engl. transl. 125 by W.G. Van Campen, 1988, 19 p., avail. Honolulu Lab., Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396].

Schnute, J.
1985 A general theory for analysis of catch and effort data. Can. J. Fish. Aquat. Sci. 42:414–429.

Ulltang, O.
1984 The management of cod stocks with special reference to growth and recruitment overfishing and the question whether artificial propagation can help to solve management problems. *In* Dahl, E., D.S. Danielssen, E. Moksness, and P. Solemdal (eds.), The propagation of cod *Gadus morhua* L., p. 795–817. Flødevigen rapp., 1.

Yatsuyanagi, K.
1982 Productive effect in stocking of prawn seedling in waters adjacent to Yamaguchi Pref. and Suho-Nada. Bull. Yamaguchi Prefect. Naikai Fish. Exp. Stn. 10:1–52.

Zheng, J., and C.J. Walters
1988 Population dynamics and stock assessment of Wanshan Spring *Decapterus maruadsi* (T.&S.) in South China Sea. Fish. Res. (Amst.) 6:217–231.

Movement, Spatial Distribution, and Mortality of Male and Female Dungeness Crab *Cancer magister* near Tofino, British Columbia

Barry D. Smith
Glen S. Jamieson

Department of Fisheries and Oceans, Biological Sciences Branch
Pacific Biological Station, Nanaimo, British Columbia V9R 5K6, Canada

Abstract. – We studied movement of Dungeness crab *Cancer magister* near Tofino, British Columbia using four methodologies. By the first two methods, beam trawling and trap sampling at specific locations, we inferred that males retreated to deeper water in winter and returned to shallower water in spring. Maturing females tended to move from coastal inlets to the more exposed coast. By the third method, a simultaneous analysis of crab movement and mortality using mark-recovery and fishing-effort data, we showed that dispersal was not extensive. Although insensitive to seasonal movement patterns, results of this analysis suggested a pattern of female movement consistent with that inferred from the beam trawl and trap data. By the fourth method, acoustic tagging, we learned that crab movement rates are inconsistent, having observed both large daily displacements (up to 925 m/day) and days of no discernible movement. The latter two analyses suggested that females tended to move about more than males, with the acoustic tagging results indicating less movement by both sexes during winter. Annual instantaneous total mortality, which is composed predominantly of natural mortality, for tagged sublegal-sized males was estimated at 2.5 (95% CI of 2.3–2.8). This is moderately less than our original natural mortality estimate of 2.9–4.5 and confirms that this original estimate was not grossly aberrant due to the confounding of movement with mortality. We estimated annual instantaneous total female mortality, which is also composed predominantly of natural mortality, to be considerably lower than that of males at 1.3 (95% CI of 0.8–1.8).

Manuscript accepted 17 October 1990.
Fishery Bulletin, U.S. 89:137–148 (1991).

The Dungeness crab *Cancer magister* is fished commercially from Alaska to central California along the Pacific coast of North America. For at least four decades this highly valued species has undergone dramatic cyclical fluctuations in commercial landings, and coincidently in population abundance (Methot and Botsford 1982), along the Pacific coast from northern California to Washington. These fluctuations have had undesirable economic consequences (Botsford et al. 1983) and potentially could result in serious biological consequences (Botsford and Wickham 1978, McKelvey et al. 1980). Therefore, there has been considerable research focused on developing an understanding of this phenomenon in recent years (Botsford 1986). Studies of this intriguing problem have been pursued methodically, with competing hypotheses systematically being eliminated (Botsford 1986). However, Methot (1986) points out that our understanding of Dungeness crab population dynamics is still limited by a lack of information on basic population processes such as growth, mortality, movement, and reproduction.

Studies of basic processes serve three purposes. Firstly, new information helps us develop a more complete understanding of complex processes. Inobvious gaps in our understanding of complex processes can cause frustrating failures to explain observed phenomena. Secondly, population models will be more realistic when supported by confident parameter estimates for key rate variables of processes generally understood. Thirdly, many studies yield data and information for which there are competing explanations, and further research is required to resolve the hypotheses in competition. A relevant example is our estimate of male Dungeness crab mortality (Smith and Jamieson 1989b) for which movement from the study site was an alternate explanation for the disappearance of tagged crabs.

The primary purpose of this paper is to report some recent progress toward understanding the movement and spatial distributions of male and female Dungeness crab. Dungeness crab population dynamics were studied near Tofino, British Columbia, where a productive regional crab fishery has existed for a number of decades. This site has been a focal point for Dungeness crab studies in British Columbia since 1985 (Jamieson and Phillips 1988, Smith and Jamieson 1989a, b, c). In addition to our studies of movement and spatial distributions, we estimated male and female mortality from a simultaneous analysis of movement and mortality of tagged crabs. The experimental design addressed the problem of movement and mortality being confounded, which plagues many studies, by including information on fishing effort.

The four methodologies we employed for assessing Dungeness crab movement yielded information at different scales of resolution. Beam trawling between June 1985 and September 1986 helped us survey the gross distribution and abundance of male and female crabs 125–140 mm carapace width (CW). Trapping helped us assess the distribution and abundance of females greater than 145 mm CW. We previously assessed male abundance and exploitation using trap sampling data in Smith and Jamieson (1989b). From the beam trawl and trapping data sets we were able to infer some seasonal movement patterns, while our model for analyzing mark-recovery data enabled us to estimate proportional transfer rates of crabs among geographical zones within our study site (see Fig. 1), and mortality. Finally, by acoustic tagging and releasing male and female Dungeness crabs during two periods, August–October 1986 and November 1986–February 1987, we were able to monitor the movement tendencies of individual crabs during summer and winter. Together, all four methodologies enabled us to document a coherent description of the spatial distribution and movement patterns of male and female Dungeness crab near Tofino, British Columbia.

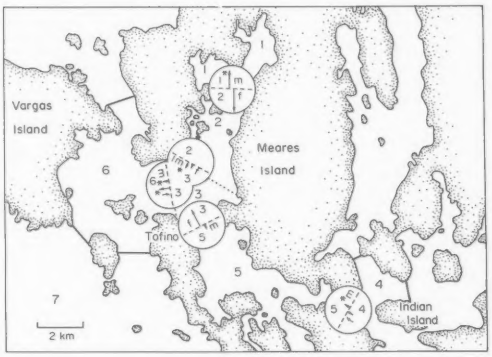


Figure 1

Map of the coastal region near Tofino, British Columbia, demarcating the geographical zones within the study site. Also shown are the relative net movement vectors across boundaries between adjacent zones for both male (m) and female (f) Dungeness crabs. The zone designation is indicated by the numbers both on the map and within the vector circle. These vectors illustrate the net directional tendencies across zone boundaries and their relative magnitude under the assumption of equal crab densities in all zones. An asterisk (*) indicates the vector magnitude is significantly ($P < 0.05$) different from zero. Zones 1–3 are in Lemmens Inlet; zone 5 is Browning Passage.

Methods

Site description

All beam trawling, trapping, and tagging were conducted within sheltered coastal waters near Tofino, British Columbia. These waters are generally ≈5–15 m depth and well mixed, with an annual seawater temperature range of ≈6–12°C. Substrate varies from sand along the exposed coast to mud near the head of Lemmens Inlet. These coastal waters have sustained a productive Dungeness crab fishery for several decades possibly due to local mudflats providing good substrate for juvenile crab (Armstrong and Gunderson 1985).

The study site is within Canadian Department of Fisheries and Oceans Statistical Area 24. The fishery in Statistical Area 24 accounted for 13 and 20% of the total weight of Dungeness crab landed in British Columbia in 1985 and 1986, respectively. During 1985 and 1986, 27 and 59 vessels, respectively, reported landings from Statistical Area 24. Of the 59 vessels which landed crab in 1986, 30 fished in the study site, and these 30 vessels accounted for approximately 80% of the 265 t landed from Statistical Area 24 in 1986. The fishery near Tofino was exploited year-round and fishing effort was sufficient to capture most males soon after their molt to legal size. Annual instantaneous fishing mortality was estimated at $F = 5.1–6.9$ (Smith and Jamieson 1989b). No crab fishing occurs in marine waters inland of the study site due to poor crab habitat.

Beam trawl sampling

In order to assess crab spatial distribution and abundance throughout the study site, we made more than 50 tows with a beam trawl (Gunderson et al. 1985, Gunderson and Ellis 1986) from June until August 1985. In addition, in areas where crabs were abundant and in a few other strategic areas, we made tows at approximately monthly intervals until September 1986. Date, tow depth, bottom type, and area swept were recorded for each tow. Crabs were sexed and their carapace widths measured. We define carapace width (CW) as the distance between the notches just anterior to the tenth anterolateral spines rounded down to the nearest millimeter. Area swept was estimated by multiplying the effective swept width of the beam trawl (2.3 m) by the distance towed. By ranging landmarks at the beginning and end of a tow of 5–10 minutes duration, we were able to calculate distance towed from high-resolution aerial photographs. Most tows were 200–500 m. Our beam trawl was assumed to be efficient and equally selective for crabs up to 135–140 mm CW. We captured very few crabs larger than 140 mm CW by beam trawl. Because it is unlikely a beam trawl captures all crabs in its path, minimum estimates of crab

densities were obtained by dividing the number of crabs captured in a tow by the area swept.

Trap sampling

The abundance of large (>145mm CW) female crabs was assessed by sampling the catch of commercial fishermen onboard their vessels. The number and carapace width of crabs caught were recorded as were the date and location of the sample. We report two indices of female abundance: n/trap · soak day and virtual catch rate (Smith and Jamieson 1989a). Virtual catch rate (n/trap · day) is the rate at which crabs would enter a trap if initial entry rates were not reduced by changes in bait effectiveness over time and agonistic interactions among crabs.

Fishing effort survey

The number of traps fished by all local fishermen, including the three fishermen who agreed to maintain records of all tagged crabs recovered in the study site, was determined by interviewing fishermen at least monthly from April 1985 until November 1986. The number of traps hauled each month in each of the seven zones demarcated in Figure 1 was estimated by incorporating trap-count data with haul-frequency data. We also maintained a record of the number of our own research trap hauls. We validated our fishing effort survey by comparing the estimated number of traps in Lemmens Inlet each month, as obtained in fishermen interviews, with the number of trap buoys we counted in Lemmens Inlet each month. With few exceptions each trap buoy indicated one trap. Trap buoys were easily counted from a moving boat on calm water in this enclosed body of water. Figure 2a compares the estimated number of traps fished in Lemmens Inlet by each method and indicates that the fishermen's interviews provided an acceptable census of trap abundance.

Mark-recovery

We tagged and released 4038 sublegal-sized male ($\bar{x}$ 142mm CW, with 95% between 106 and 162mm CW) and 1246 female ($\bar{x}$ 150mm CW, with 95% between 135 and 160mm CW) Dungeness crabs from April 1985 to May 1986. Blue, individually numbered, 4.1-cm T-bar anchor tags (Floy Tag and Manufacturing Company, Seattle, WA) were inserted through the right posterior epimeral suture line, taking care not to puncture internal organs. Crabs to be tagged were obtained from research traps, fishermen, or beam trawls. Before being released, the date, location and tag number were recorded, the crabs were sexed, and their carapace width measured. Release and recovery locations were determined with a grid identification system (0.9 × 1.2km) and landmarks.

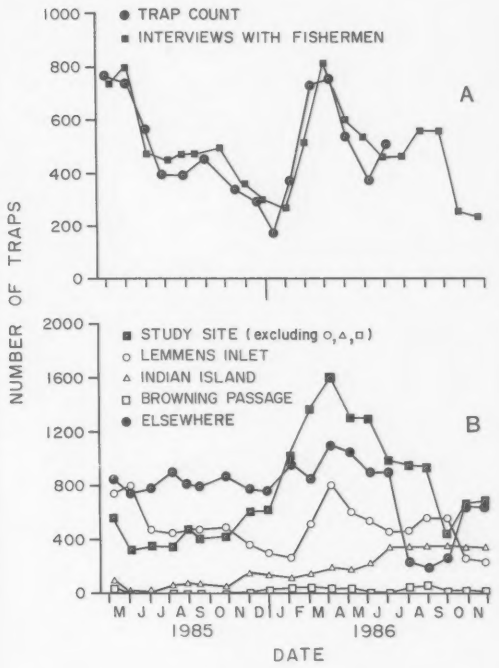


Figure 2

(A) Time-series comparison of the number of trap buoys counted in Lemmens Inlet and the number of traps estimated to be in Lemmens Inlet (zones 1–3) from interviews with fishermen. (B) Time-series of the number of traps estimated to be fishing in different regions within the study site from interviews with fishermen. 'Elsewhere' refers to traps fished outside the study site (zone 7) by fishermen who also fish within the study site.

Most recoveries were obtained from fishermen and research traps. Three fishermen recorded the date, location, and tag number of all tagged crabs they recovered on special recovery forms. Females and sublegal-sized males were returned to the water, but legal-sized males (i.e., >154mm CW) were generally retained. We asked other fishermen to ignore the recoveries of sublegal-sized crabs, i.e., return them to the water, but to retain tags from legal-sized males. Tags were either given to us or our associates, or we had permission to board a fisherman's vessel at the dock and retrieve tags set aside. From April until August of 1985 and 1986 we saw most fishermen at least biweekly, at other times monthly.

Table 1
Zone area (km²), fishing effort (trap hauls/month), fishing intensity (trap hauls/month · km²), and number of tagged male and female Dungeness crabs released for geographical zones 1–7 (Fig. 1).

Zone	Area	Fishing effort	Fishing intensity	No. of tagged crabs released	
				Male	Female
1	1.23	2234	1734	1438	160
2	0.98	8655	8823	1685	286
3	0.40	16165	40718	537	76
4	0.68	9606	14106	101	95
5	1.31	1053	801	84	11
6	7.56	25294	3345	193	618
7	10^6	15736	0.0157	0	0

Analysis of movement and mortality

We simultaneously analyzed crab movement and mortality using a model structure that facilitated estimation of monthly proportional transfer rates of crabs among the seven geographical zones demarcated in Figure 1. Zone 7 essentially represents the universe outside the study site and provides the option for crabs to vacate the study site. Maximum-likelihood parameter estimates for the transfer rates and mortality were obtained by minimizing the discrepancy between observed and expected number of recoveries in each zone during consecutive one-month intervals of time-at-large. Estimation of expected numbers of recoveries required our fishing-effort survey data. This model structure allowed us to search for persistent directional movement patterns and obtain male and female mortality estimates that were not confounded by movement of tagged crabs from the study site or into a zone where fishing effort was low.

We organized 920 male and 103 female tag recoveries by the three fishermen and ourselves who recorded all tag-recovery information, and whose fishing effort over time was measured, into frequency cells (O_{ijk}) by zone released ($i = 1,...,7$), zone recovered ($j = 1,...,7$), and months-at-large ($k = 1,...,18$). Therefore, if the observed number of recoveries in cell $O_{4,1,2} = 5$, then 5 crabs released in zone 4 were recovered in zone 1 after 2 months (30–60 days)-at-large. We ignored absolute time, so our analysis was not sensitive to seasonal movement patterns. We also assumed an equal number of trap hauls each month. Although the total number of trap hauls peaks in summer due to an increase in the number of part-time fishermen (Fig. 2b), our assumption is reasonable for the three full-time fishermen, and ourselves, whose tag-recovery and trap-haul data are the only trap-haul data incorporated into this analysis. Monthly fishing intensity (Ricker 1975) for each zone was calculated by dividing the number of trap hauls each month by the area (km²) of the zone (Table 1). Zone 7 was deliberately defined to represent an extremely large area (1 million km²) to ensure that we did not underestimate the rate of movement of tagged crabs from the study site.

The number of tagged crabs initially released in zone i that are present in zone j after k months-at-large (N_{ijk}) is described by the following series of difference Equations (1a–g).

$$N_{i1,k+1} = (N_{i1k}(1 - \Omega_{12}) + \Omega_{21}N_{i2k})s \quad (1a)$$

$$N_{i2,k+1} = (N_{i2k}(1 - \Omega_{21} - \Omega_{23}) + \Omega_{12}N_{i1k} + \Omega_{32}N_{i3k})s \quad (1b)$$

$$N_{i3,k+1} = (N_{i3k}(1 - \Omega_{32} - \Omega_{35} - \Omega_{36}) + \Omega_{23}N_{i2k} + \Omega_{53}N_{i5k} + \Omega_{63}N_{i6k})s \quad (1c)$$

$$N_{i4,k+1} = (N_{i4k}(1 - \Omega_{45}) + \Omega_{54}N_{i5k})s \quad (1d)$$

$$N_{i5,k+1} = (N_{i5k}(1 - \Omega_{53} - \Omega_{54}) + \Omega_{45}N_{i4k} + \Omega_{35}N_{i3k})s \quad (1e)$$

$$N_{i6,k+1} = (N_{i6k}(1 - \Omega_{63} - \Omega_{67}) + \Omega_{36}N_{i3k})s \quad (1f)$$

$$N_{i7,k+1} = (N_{i7k} + \Omega_{67}N_{i6k})s \quad (1g)$$

In these equations, Ω_{ij} represents the proportion of tagged crabs in zone i that move to zone j during any one-month interval. Note that when $i = j$, N_{ij0} is number of tagged crabs released in zone i (Table 1), and that Ω_{ij}'s exist only for adjacent zones (Fig. 1). The parameter Ω_{76} could not be estimated because no tagged crabs were released in zone 7. The parameter s is monthly survival rate. The annual instantaneous rate of disappearance of tagged crabs (S) is related to s by

$$S = -12\log_e[s]. \quad (2)$$

Consequent to Equations (1a–g), the expected number of recoveries of tagged crabs released in zone i and recovered in zone j after k months-at-large (E_{ijk}) is

$$E_{ijk} = N_{ijk}\, qI_j \quad (3)$$

where I_j is monthly fishing intensity (Table 1) in zone j, and q is the catchability coefficient (Ricker 1975).

We employed a multinomial negative log-likelihood function, the separation statistic

$$f_1 = \sum_{ijk} O_{ijk}\log_e[O_{ijk}/E_{ijk}], \text{ for all } O_{ijk}>0 \quad (4)$$

of Schnute and Fournier (1980), without their factor 2, to evaluate the parameter estimates. In total, the 11 Ω_{ij}'s in Equations (1a–g), q and S required estimation. The model was structured to constrain the Ω_{ij}'s to values between 0 and 1, and to assure the multinomial likelihood condition of

$$\sum_{ijk} O_{ijk} = \sum_{ijk} E_{ijk}. \quad (5)$$

Equation (4) measures the discrepancy between observed (O_{ijk}) and expected (E_{ijk}) frequencies over all frequency cells, and yields maximum-likelihood parameter estimates when f_1 is minimized. We used the SIMPLEX algorithm of Nelder and Mead (1965) as implemented by Mittertreiner and Schnute (1985) to minimize f_1, while approximate standard errors for the estimates were calculated using the numerical method supplied with Mittertreiner and Schnute (1985). This method uses the matrix of second partial derivatives of f_1 with respect to the parameters (calculated numerically) to generate the asymptotic covariance matrix (Kendall and Stuart 1979). For males we applied the analysis only to recoveries obtained after at least one full month-at-large (k>1), because tagged males were released a short time before fisherman were prepared for the mark-recovery program. Consequently our analysis of male movement and mortality is based on a sample size of 864 recoveries rather than the complete sample of 920 recoveries.

Acoustic tagging

Freshly activated acoustic tags (Smith-Root Inc., Vancouver, WA) were attached longitudinally to the carapace of recently trap-caught hard-shelled male and female Dungeness crabs using fast-drying epoxy. Care was taken to maintain each crab cool and moist while the carapace was allowed to air-dry for a short period prior to attachment of the tag. Once the epoxy set and we were confident the bond was secure (about one-half hour), each crab was placed in a bucket with fresh seawater to assess its vitality. No crabs appeared to suffer an obvious detriment from the tagging procedure, so all crabs released were anticipated to survive and transmit location information.

Once activated, each 61 × 14 mm capsule-shaped acoustic tag emits an acoustic signal characterized by a unique transmitting frequency and pulse rate. The bulk of the tag structure is a battery with a transmitting life of ≈60–90 days. With our direction-finding equipment we were able to identify a strong signal up to ≈1 km away and subsequently home-in on the location of a tag by audibly or electronically evaluating changes in signal strength. In our study site we were generally able to define the location of a tag to within ≈10–25 m of a chart reference.

During 7–13 August 1986 two male and three female crabs were tagged with acoustic tags, then released near the mouth of Lemmens Inlet (zone 3, Fig. 1). Similarly on 15 November 1986 two male and three female crabs were again tagged and released in the same area. Following the first series of releases we attempted to monitor the location of each crab at least daily, but other commitments, and occasionally being unable to locate the transmitted signal, resulted in the time between observations often exceeding one day. The same limitations applied to the second series of releases, and additionally we only attempted to monitor each crab every three days. All crabs released provided location information for 21–86 days, with the exception of a 140-mm CW male released on 15 November 1986 which was never located after its release.

Mean daily displacement rates for males and females were estimated under the assumption that movement was random from the point of release. We could not entertain a more sophisticated hypothesis with our limited data. Also because of our limited data, we report our results for males and females, and by series (August–October, November–February), with all data from individual crabs combined. Mean daily displacement is the mean expected distance between the location of a crab at the same time on two consecutive days. The maximum-likelihood estimates for mean daily displacement rates (A) were obtained by minimizing the negative log-likelihood function

$$f_2 = \sum_{i=1}^{n} \{(D_i^2/t_i A) + \log_e[t_i A^2] - \log_e[2D_i]\},$$

$$\text{for all } D_i>0 \quad (6)$$

where n is the number of observations, and D_i is the linear displacement after t_i days for crab i. When our best measurement for any D_i was zero, we assumed a minimum D_i of 1 m so that Equation (6) was defined for all data points i = 1,...,n. Our Equation (6) is the maximum-likelihood solution to Equation (3) of Skellam (1951), or Equation (11.6) of Pielou (1977), both of whom develop a mathematical framework for describing random dispersal of individuals from a release point. As for our analysis of movement and mortality, f_2 was minimized and approximate standard errors for A were determined using Mittertreiner and Schnute's (1985) SIMPLEX package.

Results

Beam-trawl and trap sampling

Beam-trawl surveys in 1985 and 1986 captured few Dungeness crabs except in the selected locations considered in the following paragraphs. In 46 beam trawl samples, 2- to 3-year-old (≈75–145 mm CW) male and female crabs (Butler 1961, Stevens and Armstrong 1984, Smith and Jamieson 1989c) were found at densities generally less than 10/hectare (ha). Where much higher densities were found, there were significant seasonal differences, and differences in the relative proportions of males and females. Sampling since 1986 in the same locations (G. Jamieson, unpubl. data) has indicated that the overall abundance of crabs in the 75–145 mm CW size range has dropped to a low level, thus we believe the pattern of spatial and temporal distribution we describe herein is based on observations of essentially one strong year-class.

In upper Lemmens Inlet the densities of male and female 2-year-olds in summer 1985 were initially low and continued to decline throughout 1985 and 1986 (Fig. 3a). This suggests this area is a poor crab habitat since this cohort was abundant elsewhere. The highest density of males was observed in middle Lemmens Inlet (Fig. 3b). During autumn 1985 and the subsequent winter, male densities steadily increased to greater than 1200/ha. Toward the mouth of Lemmens Inlet male densities generally declined (Fig. 3c, d). Because densities of 2-year-old males elsewhere were consistently low, the increase in the number of males in middle Lemmens Inlet is suspected to be due to movement away from exposed shallow water during winter.

We suspect that these males concentrated in middle Lemmens Inlet because of poor habitat further up the inlet. This high density of males eventually decreased rapidly during late spring 1986. Most males were in the normally distributed instar with a mean carapace width of 129 mm and a standard deviation of 12 mm (Smith and Jamieson 1989c), and many molted to legal size in 1986 (i.e., to the normally distributed instar with a mean carapace width of 156 mm and a standard deviation of 13 mm). Following their molt to legal size they were quickly caught in an intense fishery (Smith and Jamieson 1989b). About 25–35% of the fishing effort in the study site was concentrated in Lemmens Inlet during spring 1986 (Fig. 2b).

A high density of 2-year-old females was observed in the narrow channel at the lower end of Lemmens Inlet in June 1985 (Fig. 3c). Density declined after this date, but increased during autumn in the entrance to Lemmens Inlet (Fig. 3d) 0.5–1.0 km seaward of the narrow channel. Female density further up Lemmens

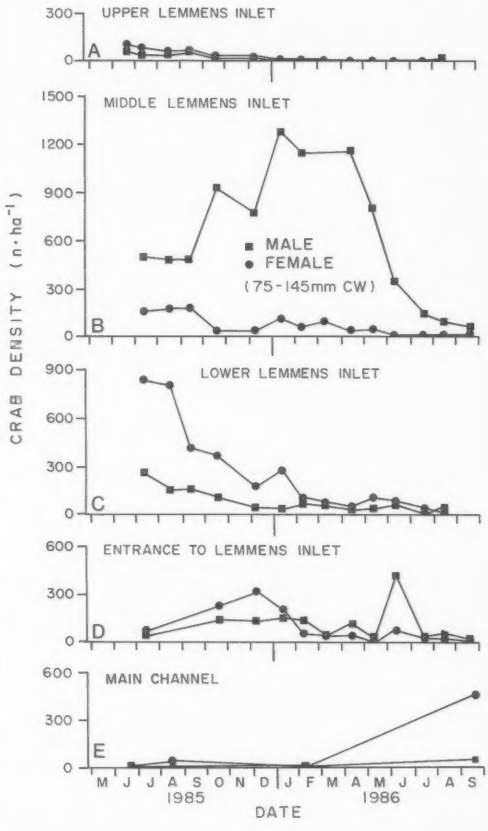


Figure 3

Time-series of densities for 2–3 year-old (≈75–145 mm CW) male and female Dungeness crabs in upper Lemmens Inlet (zone 1), middle Lemmens Inlet (zone 2), lower Lemmens Inlet (zone 2), the entrance to Lemmens Inlet (zone 3), and in the main channel out to sea (zone 6).

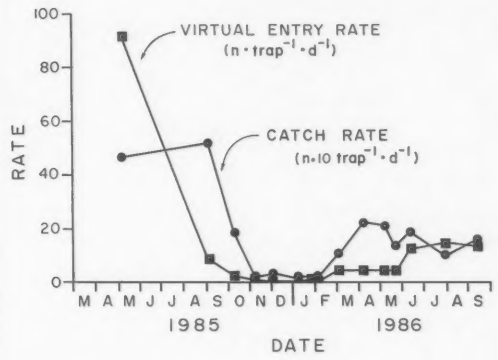


Figure 4

Two indices of abundance for female Dungeness crabs >145 mm CW in zone 6, where females were most abundant (Table 2). The virtual catch rate is the rate at which females would enter a trap if entry rates were not modified by changes in bait effectiveness over time and agonistic interactions among crabs (see Smith and Jamieson 1989a).

Table 2

Abundance (n/100 traps · soak day) of female Dungeness crabs >145 mm CW in commercial traps during May and June of 1985 and 1986.

	Female abundance	
Area samples	1985	1986
Upper Lemmens Inlet (zone 1)	7	13
Lemmens Inlet (zones 2 and 3)	15	8
Browning Passage (zone 5)	22	4
Near Indian Island (zone 4)	10	36
Main channel (zone 6)	429	138

Table 3

Maximum-likelihood estimates and standard errors (SE) of the proportion (Ω_{ij}) of tagged male and female Dungeness crabs in zone i transferring to an adjacent zone j during a one-month interval. Asterisks indicate transfer proportions significantly ($P<0.05$) greater than zero.

	Male		Female	
Parameter	Proportion	SE	Proportion	SE
Ω_{12}	0.15*	0.02	0.84*	0.25
Ω_{21}	0.50*	0.09	0.68*	0.13
Ω_{23}	0.22*	0.02	0.10*	0.03
Ω_{32}	0.16*	0.03	0.07	0.07
Ω_{35}	0.44*	0.06	0.22	0.12
Ω_{53}	0.11*	0.02	0.36	0.27
Ω_{36}	0.40*	0.04	0.63*	0.12
Ω_{63}	<0.01	<0.01	<0.01	<0.01
Ω_{45}	0.12*	0.03	0.01	0.01
Ω_{54}	<0.01*	<0.01	0.09	0.08
Ω_{67}	0.04*	0.01	0.02	0.01

Inlet continued to decline, suggesting seaward movement. The increase in female abundance in September 1986 where the main channel out of the study site meets the open coast (Fig. 3e) also suggests seaward movement of females. These females were inferred to be 3-year-olds because they were mainly in the normally distributed instar with a mean carapace width of 137 mm and a standard deviation of 9 mm (Smith and Jamieson 1989c).

The relative abundance of larger females in the study site was assessed by trap sampling. Two indices of abundance obtained from commercial trap samples (Fig. 4), show that females were most readily caught in spring, perhaps because they forage more actively after a winter of incubating eggs. The highest observed abundance of the larger females (>145 mm CW) in spring 1985 and 1986 (Table 2) was in the main channel out of the study site. This is also where (presumably) 3-year-old females in the 137 mm instar were collected in abundance by beam trawl in September 1986. This is consistent with the suggestion from beam-trawl sampling of seaward movement from local inlets as females mature.

Analysis of movement and mortality

Our estimate of the catchability coefficient q for females of 0.198×10^{-5} recoveries per trap haul was about one-seventh that for males (0.138×10^{-4} recoveries per trap haul), indicating males were much more readily caught than females by commercial traps. This difference is mainly due to commercial traps being more efficient at retaining larger crabs which are predominantly males. Consequently it is apparent in Table 3 that our transfer proportion estimates for females are much less confidently made than those for males because of the much smaller number of tagged females recovered.

The proportional transfer rates for males do not suggest any persistent directional movement. We note that there is little transfer of crabs between Indian Island (zone 4) and Browning Passage (zone 5) when compared with the apparent mixing among zones 1, 2, 3, 5, and 6, so the movement of tagged crabs through the deeper water between Browning Passage and Indian Island appears limited. Male crabs appear to vacate middle and lower Lemmens Inlet (zones 2 and 3) at proportional rates of about 0.22 and 0.40 per month with

only a small proportion per month (0.01) entering Lemmens Inlet from zone 6. The monthly proportional transfer rate of crabs from zone 2 to zone 1 (Ω_{21}) of 0.50 seems high compared with transfer of crabs from zone 1 to zone 2 (Ω_{21}) of 0.15, but this might be explained by zone 1 (upper Lemmens Inlet) being poor crab habitat and the possibility that only a small proportion of male crabs are successful in escaping this habitat.

The proportional transfer rates for females have large standard errors and must be interpreted cautiously. However, a notable result is the 0.63 proportional transfer rate for Ω_{36} compared with <0.01 for Ω_{63}, thus indicating that a greater proportion of tagged females vacated lower Lemmens Inlet than entered Lemmens Inlet. The monthly proportional transfer rate of 0.84 for females escaping the poor habitat in zone 1 (Ω_{12}) is high compared with males, but might indicate females are more capable of recognizing the environmental clues leading to more suitable substrate. The transfer rates of females in both directions between zone 1 and zone 2 are notably higher than the male transfer rates, and since the largest release of tagged male and female crabs was in zones 1 and 2, this result might indicate females are generally more mobile than males.

Proportional transfer rates alone are an incomplete interpretation of movement trends, since the zones differ in area and therefore also in crab abundance. Consequently, the high transfer rate for Ω_{36} when compared with Ω_{63} is in large part a result of zone 6 having an area of 7.56 km^2, whereas zone 3 has an area of 0.40 km^2. Relative movement vectors were therefore calculated from the transfer-rate estimates under the assumption that crab densities were equal for all zones. For example, if crab density is Δ crabs per km^2, then the estimated number of crabs transferring from zone 6 to zone 3 in a one-month period is $7.56\Delta\Omega_{63}$.

Figure 1 diagrams net movement tendencies, under the assumption of equal crab densities in all zones, across those zone boundaries where transfer rates in both directions were estimated. Two notable features for males are the strong indication of net movement of males into upper Lemmens Inlet, and a tendency for males to vacate lower Lemmens Inlet and the waters near Indian Island. As previously mentioned, the net movement into upper Lemmens Inlet might be a result of a low proportion of males escaping this poor habitat. It might also indicate dispersion from zone 2 where many males were tagged and released in spring 1986. A large number of males 125–140 mm CW were tagged in zone 2 in spring 1986 because they occurred in high density (>1200/ha) and were readily captured by beam trawl. Beam trawling indicated these crabs apparently dispersed, or molted to legal size and were caught, by summer 1986 (see previous section). For females there is a general, although non-significant, tendency to vacate Lemmens Inlet and Browning Passage. This result is consistent with our beam-trawl and trapping results (previous section) which also demonstrate a net seaward movement of females from Lemmens Inlet.

Table 4

Maximum-likelihood estimates and standard errors (SE) of mean daily displacements (A, m/d) of male and female Dungeness crabs.

	Male			Female		
	n	Estimate	SE	*n*	Estimate	SE
Aug 86–Oct 86	31	321	29	30	500	45
Nov 86–Feb 87	8	74	13	15	161	21
Combined	39	288	23	45	419	31

We estimated the annual rate of disappearance of tagged crabs with reasonable confidence at S = 2.54 (SE 0.13) and S = 1.28 (SE 0.27) for males and females, respectively. Corroborating these high estimates for S, our analysis estimated that only about 2% and 7% of tagged males and females, respectively, left zones 1–6, i.e., moved to zone 7, over the time-period of our study. In other words, the distribution over time of tag recoveries in zones 1–6 could not be well explained by a high transfer rate into zone 7 where crabs might not be recovered due to a low fishing intensity. Thus these estimates for S were obtained despite our model structure providing an exaggerated opportunity for crabs to disperse to zone 7 as an alternative explanation for the disappearance of tagged crabs, i.e., as an alternative to mortality. This conclusion appears to validate our original assumption that few tagged crabs left our study site during the study period (Smith and Jamieson 1989b).

Based on a double-tagging study, Smith and Jamieson (1989b) concluded that tag loss by sublegal-sized crabs is low and therefore unlikely to be an important source of tag disappearance. Observations of tank-held crabs over several months did not reveal differential mortality of tag and untagged crabs. Thus we conclude that the values for S estimated in this study represent mainly natural mortality and, in the case of males, tag disappearance due to molting to legal size with subsequent exploitation. However, because only about 5% of tagged sublegal-sized males were reported caught as legal-sized crabs (210 recovered when legal-sized of the 4038 released when sublegal-sized), despite high fishing mortality (F = 5.1–6.9) and apparently good compliance in reporting recovered tags (≈87%), we con-

clude that our male estimate for S measures mainly natural mortality of sublegal-sized males. We recognize, however, that there is likely some degree of mortality due to trapping and handling by fishermen. Similarly, and in consideration that females are not commercially fished, we are confident that our female estimate for S also mainly measures natural mortality.

Acoustic tagging

From the means and standard errors of the movement rate estimates (Table 4) we conclude that for both the August and November 1986 releases of acoustically tagged crabs, females tended to move about significantly ($P<0.01$) more than males. Similarly, during August–October 1986 both males and females seemed to move at rates about 3 to 4 times faster ($P<0.01$) than those for November 1986–February 1987. We realize, however, that our male results for the latter time period are based on observations of just one crab. Slower movement during winter for both male and female crab is consistent with the poikilothermic habit of marine invertebrates in that respiratory activity is closely related to temperature. Our analysis of movement based on the mark-recovery data also hints that females are more mobile than males.

We cannot conclude that our estimate of a faster movement rate for females, relative to males, represents a general phenomenon for all Dungeness crab populations. Our acoustic tagging results are possibly peculiar to our study site, since the greater movement rate for females is consistent with our interpretation of the trapping and beam trawl results which suggest that females tend to vacate the coastal inlets in search of the exposed coast. Further, we caution that our dispersal rate estimates for males and females from the acoustic tagging data should be considered minimum estimates because the archipelago in which the acoustically tagged crabs were released will tend to restrict the potential for movement. Also, our assumption of random dispersal from the point of release of an acoustically tagged crab is probably too strict. Our beam trawl and trapping data indicate that both males and females might move in response to environmental clues such as tides and currents; and our beam-trawl, trapping, and mark-recovery data all suggest seaward movement of females from Lemmens Inlet.

These limitations to our interpretation of the acoustic tagging data preclude us from obtaining precise rates of population dispersal over time. However, we think that there is some value in presenting approximate dispersal rates since they can be compared with the results of our analysis of movement and mortality, and to some degree with Dungeness crab movement rates that might be obtained from other regions. Consequently, the mean daily displacement rates (A) of 288 m/day and 419 m/day obtained for males and females, respectively, suggest that after one year of random dispersal, in the absence of geographical boundaries, 95% of males and females would be within radii of 9.5 and 13.9 km, respectively, of the point where they were one year previous. These radii were determined from

$$r^2 = -\log_e[p_{rt}]A^2t \qquad (7)$$

where r is the radius within which the proportion $1 - p_{rt}$ of a randomly dispersing population is expected after t days (Pielou 1977). These estimates of r agree favorably with the results of our simultaneous analysis of movement and mortality from our mark-recovery data in that about 2% and 7% of male and female crabs, respectively, were estimated to leave the study site during the 18-month study period. The study site encompasses an area of about 5–10 km radius around Tofino (Fig. 1).

Discussion

The four methodologies we employed to assess male and female Dungeness crab movement provided insights at different levels of resolution and from different perspectives. The methodologies were complementary and together allowed us to document a coherent description of Dungeness crab movement near Tofino, British Columbia. For example, acoustic tagging gave us a general indication of the dispersal rates for individual male and female crabs (summer and winter) which was consistent with the results of our simultaneous analysis of movement and mortality using mark-recovery data. The former analysis suggested that the dispersal rates would maintain 95% of the male and female populations within about 10 km and 14 km, respectively, of points of release, while the latter analysis suggested that only about 2% of males and 7% of females would escape the study site (about 10–15 km radius) during our 18-month study period. In addition, both the beam-trawl and trap samples documented seasonal changes in the relative distributions and abundances of males and females which could not be gleaned from the acoustic tagging and mark-recovery data alone.

Overall, our four sources of movement information suggest that male Dungeness crab undergo only limited movements within the local archipelago. There was no evidence of migratory movement, but males were inferred to move to shallower water (≈10 m) during summer, then to retreat to more sheltered habitat in autumn. Others have observed, or inferred, similar behavior for this species. Stevens and Armstrong (1984)

reported that juvenile males and females of the 1980 year-class in Grays Harbor, Washington, disappeared during the winter of their first year, then reappeared the following spring. Gotshall (1978) observed movement of sublegal- and legal-sized male crabs in northern California to deeper water in winter, and a return to shallower water in spring. It is reasonable to surmise that the autumn movement to deeper water is to avoid rough shallow water during the winter. Returning to shallower, warmer, and more productive water during summer could enhance growth and survivorship.

Our estimated average daily displacement rate for male Dungeness crabs of ≈300 m/day, is consistent with our inferences on movement from our mark-recovery, beam-trawl, and trap sampling results. Our general conclusion of limited movement is also consistent with the results of other tagging studies. Both Butler (1957) for Dixon Entrance, British Columbia, and Gotshall (1978) for northern California, suggested that Dungeness crab populations remain local. With the exception of the apparent seasonal shift in habitat, no studies suggest migratory movements for males; however, Gotshall (1978) noted that males seem to move in the direction of prevailing currents off northern California. Bennett and Brown (1983) report that most tagged males of the closely related crab *Cancer pagurus* remained near where they were released in the English Channel.

Our acoustic tagging and mark-recovery data suggest that female Dungeness crab undergo only limited movement. Diamond and Hankin (1985) similarly argued that mature female Dungeness crab off the coast of northern California undergo limited movements and suggested that females constitute localized stocks. Diamond and Hankin (1985) do suspect that females move short distances to shallower water in spring to mate and molt. Our analyses provided no evidence of this, but it is quite conceivable that both males and females could improve mating opportunities by concentrating in shallow water (Butler 1960).

We inferred, mainly from our beam trawl and trap samples, that females tended to move from coastal inlets to an area more exposed to the open coast (zone 6, Fig. 1). In the inlets the substrate ranged from mud to a mud/sand mix, whereas in the more exposed area the bottom was mainly sand or a sand/gravel mix. Wild (1980) states that females must be at least partially buried in sandy substrate to extrude and incubate eggs so our inference is consistent with the current understanding of the life history of Dungeness crab females. Stevens and Armstrong (1984) noted that egg-bearing females were rare in Grays Harbor, and speculated that most mature females left the harbor to incubate and release their eggs in a preferred environment. Our study yielded an average daily displacement rate for females (≈400 m/day) which was significantly ($P<0.01$) more than the rate for males (≈300 m/day), and which might be explained by females undergoing deliberate migratory movements to locate suitable substrate for incubating eggs.

Similar movement behavior has been reported for females of other crab species. Hyland et al. (1984) observed the movement of female portunid crab *Scylla serrata* from an estuarine environment, where they lived as juveniles, to the open ocean where they released their eggs. Some females returned to inshore waters after the hatching season. Bennett and Brown (1983) demonstrated that female *C. pagurus* undergo extensive movements, apparently to locate habitat more suitable for egg incubation and release. While SCUBA diving, Howard (1982) observed egg-bearing female *C. pagurus* congregated in relatively deep (24 m), quiet water. Since they were rare elsewhere, he concluded this was a preferred habitat. Dinnel et al. (1987) observed a similar behavior for Dungeness crab in Puget Sound, Washington, from the Government of Canada submersible *Pisces IV*.

Our simultaneous analysis of Dungeness crab movement and mortality using mark-recovery and fishing-effort data diminished the confounding of these two processes and yielded a revised estimate of the natural mortality rate originally proposed by Smith and Jamieson (1989b). Our (mainly) natural mortality rate estimate for males of 2.5 (95% CI of 2.3–2.8) is moderately lower than our previous estimate of 2.9–4.5, probably because of dispersal of tagged crabs into zones (especially zone 6) with low fishing intensities.

Our estimate of female natural mortality of 1.3 (95% CI of 0.8–1.8) is significantly lower than that of males but in general agreement with the mortality estimates of Hankin et al. (1985, 1989) for females in northern California. They estimated annual instantaneous natural mortality for females greater than 140 mm CW at 2.0 and 2.5 for two different periods of release in a mark-recovery experiment. For females 125–140 mm CW their rough estimate was ≈0.7, a more precise estimate being unobtainable due to females this size having a high probability of molting and changing vulnerability to traps. Our estimate of 1.3 is based on a group of tagged females whose carapace widths at release were 135–171 mm ($\bar{x}$ 150 mm), thus our estimate seems consistent with those of Hankin et al. (1985, 1989).

The estimates of male and female natural mortality from this study, and of female natural mortality from Hankin et al. (1985, 1989), for crabs near the Canadian minimum legal size limit of 154 mm CW (165 mm spine-to-spine CW) increases our confidence that mortality of mature Dungeness crab is indeed high. For example, a mortality rate of 2.0 means only 13.5% annual

survivorship. The recognition of such a high mortality rate for adults of this commercially important species immediately prompts questions regarding the appropriateness of both the Canadian and American (≈159 mm CW) minimum legal carapace width limits for optimizing two of the most basic stock-management guidelines: yield-per-recruit and eggs-per-recruit.

Acknowledgments

We are grateful to Messrs. A. Phillips, D. Heritage, and W. Harling who provided most of the field support, and to Dr. L.J. Richards and Mr. J. Fulton who reviewed a previous version of this paper. We extend special thanks to the fishermen of Tofino who participated in the mark-recovery program and expressed a keen interest in our activities.

Citations

Armstrong, D.A., and D.R. Gunderson
1985 The role of estuaries in Dungeness crab early life history: A case study in Grays Harbor, Washington. *In* Melteff, B.R. (ed.), Proceedings of the symposium on Dungeness crab biology and management, p. 145–169. Alaska Sea Grant Rep. 85-3, Univ. Alaska, Fairbanks.

Bennett, D.B., and C.G. Brown
1983 Crab (*Cancer pagurus*) migrations in the English Channel. J. Mar. Biol. Assoc. U.K. 63:371–398.

Botsford, L.W.
1986 Population dynamics of the Dungeness crab (*Cancer magister*). *In* Jamieson, G.S., and N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates, p. 140–153. Can. Spec. Publ. Fish. Aquat. Sci. 92.

Botsford, L.W., and D.E. Wickham
1978 Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35:833–843.

Botsford, L.W., R.D. Methot Jr., and W.J. Johnston
1983 Effort dynamics of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 40: 337–346.

Butler, T.H.
1957 The tagging of the commercial crab in the Queen Charlotte Islands region. Fish. Res. Board Can. Pac. Prog. Rep. 109:16–19.
1960 Maturity and breeding of the Pacific edible crab, *Cancer magister* Dana. J. Fish. Res. Board Can. 17:641–646.
1961 Growth and age determination of the Pacific edible crab *Cancer magister* Dana. J. Fish. Res. Board Can. 18:873–889.

Diamond, N., and D.G. Hankin
1985 Movements of adult female Dungeness crabs (*Cancer magister*) in northern California based on tag recoveries. Can. J. Fish. Aquat. Sci. 42:919–926.

Dinnel, P.A., D.A. Armstrong, R.R. Lauth, and G.S. Jamieson
1987 Use of the PISCES IV submersible for determining the distributions of Dungeness crab, shrimp, and bottomfish in Port Gardner, Washington. Fish. Res. Inst. Final Rep. FRI-UW-8709, Univ. Wash., Seattle, 16 p.

Gotshall, D.W.
1978 Northern California Dungeness crab, *Cancer magister*, movements as shown by tagging. Calif. Fish Game 64: 234–254.

Gunderson, D.R., and I.E. Ellis
1986 Development of a plumb staff beam trawl for sampling demersal fauna. Fish. Res. (Amst.) 4:35–41.

Gunderson, D.R., D.A. Armstrong, and C. Rogers
1985 Sampling design and methodology for juvenile Dungeness crab surveys. *In* Melteff, B.R. (ed.), Proceedings of the symposium on Dungeness crab biology and management, p. 135–144. Alaska Sea Grant Rep. 85-3, Univ. Alask, Fairbanks.

Hankin, D.G., N. Diamond, M. Mohr, and J. Ianelli
1985 Molt increments, annual molting probabilities, fecundity and survival rates of adult female Dungeness crabs in northern California. *In* Melteff, B.R. (ed.), Proceedings of the symposium on Dungeness crab biology and management, p. 189–206. Alaska Sea Grant Rep. 85-3, Univ. Alaska, Fairbanks.

Hankin, D.G., N. Diamond, M.S. Mohr, and J. Ianelli
1989 Growth and reproductive dynamics of adult female Dungeness crabs (*Cancer magister*) in northern California. J. Cons. Cons. Int. Explor. Mer 46:94–108.

Howard, A.E.
1982 The distribution and behavior of ovigerous edible crabs (*Cancer pagurus*), and consequent sampling bias. J. Cons. Cons. Int. Explor. Mer 40:259–261.

Hyland, S.J., B.J. Hill, and C.P. Lee
1984 Movement within and between different habitats by the portunid crab *Scylla serrata*. Mar. Biol. (Berl.) 80:57–61.

Jamieson, G.S., and A.C. Phillips
1988 Occurrence of *Cancer* crab (*C. magister* and *C. oregonensis*) megalopae off the west coast of Vancouver Island, British Columbia. Fish. Bull., U.S. 86:525–542.

Kendall, M., and A. Stuart
1979 The advanced theory of statistics, Vol. 2. Inference and relationship, 4th ed. MacMillan, NY, 748 p.

McKelvey, R., D. Hankin, R. Yanosko, and C. Snygg
1980 Stable cycles in multistage recruitment models: An application to the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 37:2323–2345.

Methot, R.D. Jr.
1986 Management of Dungeness crab fisheries. *In* Jamieson, G.S., and N. Bourne (eds.), North Pacific workshop on stock assessment and management of invertebrates, p. 326–334. Can. Spec. Publ. Fish. Aquat. Sci. 92.

Methot, R.D. Jr., and L.W. Botsford
1982 Estimated preseason abundance in the California Dungeness crab (*Cancer magister*) fisheries. Can. J. Fish. Aquat. Sci. 39:1077–1083.

Mittertreiner, A., and J. Schnute
1985 Simplex: A manual and software package for easy nonlinear parameter estimation and interpretation in fishery research. Can. Tech. Rep. Fish. Aquat. Sci. 1384, 90 p.

Nelder, J.A., and R. Mead
1965 A simplex method for function minimization. Computer J. 7:308–313.

Pielou, E.C.
1977 Mathematical ecology. John Wiley, NY, 384 p.

Ricker, W.E.
1975 Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Schnute, J., and D. Fournier
1980 A new approach to length frequency analysis: Growth structure. Can. J. Fish. Aquat. Sci. 37:1337–1351.

Skellam, J.G.
1951 Random dispersal in theoretical populations. Biometrika 38:196–218.

Smith, B.D., and G.S. Jamieson
1989a A model for standardizing Dungeness crab (*Cancer magister*) catch rates among traps which experienced different soak times. Can. J. Fish. Aquat. Sci. 46:1600–1608.
1989b Exploitation and mortality of male Dungeness crabs (*Cancer magister*) near Tofino, British Columbia. Can. J. Fish. Aquat. Sci. 46:1609–1614.
1989c Growth of male and female Dungeness crabs near Tofino, British Columbia. Trans. Am. Fish. Soc. 118:556–563.

Stevens, B.G., and D.A. Armstrong
1984 Distribution, abundance, and growth of juvenile Dungeness crabs, *Cancer magister*, in Grays Harbor estuary, Washington. Fish. Bull., U.S. 82:469–483.

Wild, P.W.
1980 Effects of seawater temperature on spawning, egg development, hatching success, and population fluctuations of the Dungeness crab, *Cancer magister*. Calif. Coop. Oceanic Fish. Invest. Rep. 21:115–120.

Abstract.– A logbook program was initiated to determine the relative abundance of selected fish species around oil and gas platforms off the Louisiana coast. Logbooks were maintained by 55 anglers and 10 charterboat operators from March 1987 to March 1988. A total of 36,839 fish were caught representing over 46 different species.

Principal component analysis (PCA) grouped the seventeen most abundant species into reef fish, pelagic fish, bluefish–red drum, Atlantic croaker–silver/sand seatrout, and cobia–shark–blue runner associations. Multiple regression analyses were used to compare PCA groupings to physical platform, temporal, geological, and angler characteristic variables and their interactions. Reef fish, Atlantic croaker, and silver/sand seatrout abundances were highest near large, structurally complex platforms in relatively deep water. High spotted seatrout abundances were correlated with small, unmanned oil and gas platforms in shallow water. Pelagic fish, bluefish, red drum, cobia, and shark abundances were not related to the physical parameters of the platforms.

Factors Affecting the Abundance of Selected Fishes near Oil and Gas Platforms in the Northern Gulf of Mexico*

David R. Stanley
Charles A. Wilson

Coastal Fisheries Institute, Center for Wetland Resources
Louisiana State University, Baton Rouge, Louisiana 70803

Louisiana has long been recognized as having abundant fisheries resources as evidenced by the large number of recreational and commercial fishing opportunities. This is particularly true of its offshore waters which Moore et al. (1970) characterized as having high densities of demersal fishes and Gunter (1963) postulated were the most productive waters on earth based on fishery harvests.

Saltwater sportfishing off Louisiana is concentrated around oil and gas platforms with an estimated 37% of all saltwater angling trips (Witzig 1986) and over 70% of all recreational angling trips in the Exclusive Economic Zone (more than 3 miles from shore) occurring around platforms (Reggio 1987). All of the 3700 oil and gas platforms off the coast of Louisiana are thought to act as artificial reefs and have contributed to Louisiana's designation as a fishing "paradise."

Gallaway (1984) estimated that oil and gas platforms constitute 28% of the known hard substrate off Louisiana and Texas. This is of particular importance off the Louisiana coast since the nearest natural hard bottom habitat is approximately 92 km from shore (Sonnier et al. 1976); therefore, oil and gas platforms provide the only source of hard-bottom habitat close to shore. The continued growth of the offshore oil and gas industry in Louisiana has provided habitat expansion for organisms dependent on hard substrate (Sonnier et al. 1976, Gallaway et al. 1981a, Continental Shelf Associates 1982).

Oil and gas platforms are unique as artificial reefs because they extend throughout the entire water column. Their effects are not confined to benthic and demersal fishes; pelagic fishes also benefit (Gallaway et al. 1981a, Continental Shelf Associates 1982). For example, pelagic baitfish (i.e., round scad *Decaptarus punctatus*, Spanish sardine *Sardinella anchovia*, and scaled sardine *Harengula pensacolae*) often maintain a position from nearsurface to mid-depth within or upcurrent from oil and gas structures feeding on plankton and zooplankton, while large predatory pelagic fishes (i.e., king mackerel and blue runner) are reported to swim from the surface to mid-depth around structures, rarely venturing within the structure (Hastings et al. 1976, Gallaway et al. 1981a).

Although oil and gas structures, like most artificial reefs, are considered to increase production and attract fish, there are few accepted techniques to assess their effectiveness. A method of testing the success or importance of an artificial reef is to track the number of fish caught over time. Due to the complex construction of oil and gas platforms, sampling with traditional fisheries

Manuscript accepted 28 September 1990.
Fishery Bulletin, U.S. 89:149–159 (1991).

*Contribution No. LSU-CFI-89-04, Louisiana State University, Coastal Fisheries Institute.

gear (e.g., trawls, gillnets) is difficult at best; therefore, the number of fish caught per angler/hour (CPUE) was used to estimate the relative abundance of fish near oil and gas platforms.

Artificial reefs have been reported to concentrate scattered fishes and/or elevate secondary production by increasing the growth and survival of new individuals. However, few studies have examined the trophodynamics of these systems (Bohnsack and Sutherland 1985). The attraction/production paradigm should not be viewed as a black and white issue, but as a gradient depending upon species, life-history stage, type of artificial reef, etc. (Bohnsack 1989). Many species of fish around oil and gas platforms are trophically independent of the structure (e.g., pelagic fishes), but may use the platform for other purposes (e.g., optical stimulus, shelter, protection from predation, seasonal movements, spawning and orientation) (Gooding and Magnuson 1967, Hunter and Mitchell 1967, Klima and Wickham 1971, Wickham et al. 1973, Gallaway et al. 1981a, Continental Shelf Associates 1982).

Factors that may explain the congregation of fish around artificial reefs are poorly known (Grove and Sonu 1983). Some theories on factors influencing the abundance and attraction of fish to artificial reefs include shape and complexity (Hunter and Mitchell 1968, Luckhurst and Luckhurst 1978, Grove and Sonu 1983, Chandler et al. 1985), size of the artificial reef (Hunter and Mitchell 1968, Huntsman 1981, Grove and Sonu 1983, Turner et al. 1969, Rousenfell 1972, Ogawa 1982, Vik 1982), age of the artificial reef and seasonality (Turner et al. 1969, Molles 1978, Stone et al. 1979, Smith 1979, Lukens 1981, Stephens and Zerba 1981). Colonization of natural and artificial reefs did not follow the MacArthur and Wilson (1967) model of species equilibrium for insular biotas according to Smith (1979) and Lukens (1981). They found the strong seasonal effects in the northern Gulf of Mexico produced seasonally stable communities with regular fluctuations in diversity and abundance.

The objective of this study was to determine if a relationship exists between the relative abundance of selected fish species near oil and gas platforms off the Louisiana coast and (1) physical platform variables (e.g., water depth, submerged surface area, volume of water enclosed by the platform, mode of platform operation, platform age), (2) temporal variables (e.g., linear, quadratic, and cubic functions of date), (3) meteorological and geological variables (e.g., air temperature, wind speed and direction, mean sediment size), and (4) angler characteristic variables (e.g., fishing method, boat length, total engine horsepower, presence of electronic fishing aids).

Materials and methods

Between September 1986 and March 1987 we solicited 120 recreational anglers from fishing clubs across Louisiana to maintain logbooks. In addition, 23 of the charterboat operators listed in National Marine Fisheries Service records and Coleman (1984) volunteered to maintain logbooks. Logbook data were collected from March 1987 to March 1988. The design of the logbook and data collected were based on the Lake Erie Angler Diary Program (Sztramko 1986) and logbook criteria outlined by Demory and Golden (1983). Information obtained from the logbooks included: date of trip, number of anglers, oil and gas platform fished, fishing time (not including travel time), fishing method, bait used, and the species and number of fish caught. Due to the difficulty in identification of some fish species, snapper other than red snapper, groupers, sharks, and silver and sand seatrout were classified as other snapper, groupers, sharks, and silver/sand seatrout respectively. Other data acquired from logbook participants included boat length (m), total engine horsepower, and the presence of electronic fishing aids (e.g., LORAN, graph recorders, and echosounders) which assisted in the capture of fish.

We also measured characteristics of the platform, surrounding sediments, and weather which we considered important. Submerged surface area (m^2), volume of water enclosed by the structure (m^3), and the number of legs, wells, and structural crossmembers for each platform utilized by the logbook participants were calculated from drawings and information provided by offshore oil operators. Water depth (m) and age of the structures were supplied by the Minerals Management Service. Surface sediment sizes (μm) adjacent to oil and gas structures were taken from Coleman et al. (1986). Meteorological data, including average daily wind speed (km/hour), direction, and temperature (°C), for the New Orleans International Airport were obtained from the Louisiana State Climatology Office.

To account for seasonal differences in abundance, linear, quadratic, and cubic orthogonal polynomials of the 12 months of the study were used. Orthogonal polynomial contrasts are by definition uncorrelated, thus enabling the unique contribution of the linear, quadratic, or cubic effects of time to be identified.

CPUE was calculated as the number of fish caught per angler per hour of fishing. Prior to any analysis that assumes data normality, the distribution of CPUE data was tested and found not to be normal. Therefore, in order to approximate the normal distribution, the CPUE data were transformed by $\ln(\text{CPUE} + 1)$ due to the large number of zero values in the original data (Pennington 1983, 1985).

Two multivariate analysis techniques were utilized to determine the relationships between species abundance and geological, physical, temporal, and meteorological variables. Principal Component Analysis (PCA) was used on the individual fish species as a data-reduction technique. The PCA transforms the original set of variables into a smaller set of orthogonal linear combinations of species that account for a major portion of the variance in the original set (Chatfield and Collins 1980, Dillon and Goldstein 1984). The CPUE data from 17 species or species groups were reduced to 5 principal components (PC's) using the FACTOR procedure (SAS 1985). Only PC loadings greater than 0.35 were considered; although the value of 0.35 is arbitrary, it implies at least 12% of the variance of the species variable was accounted for by the PC. The component scores of the five PC's were used in subsequent multiple-regression analyses.

Stepwise multiple-regression analyses (MRA) were performed with spotted seatrout ln(CPUE + 1) and the component scores of each PC on the angler characteristics, meteorological, temporal, geological, and physical platform data and their interactions (predictor variables) (Table 1). An MRA of the predictor variables and ln(CPUE + 1) of spotted seatrout was treated as a separate analysis because spotted seatrout represented 24.8% and 28.3% of the total number of fish caught by anglers and charterboat operators, respectively (Table 2), and because they did not load positively with the other species in the PCA. The MRA was executed using the STEPWISE procedure with the MAXR option in SAS (1985). Unless otherwise stated, all differences discussed are significant at the $\alpha = 0.01$ level of significance.

Table 1

Temporal, meteorological, angler characteristic, physical platform, and geological variables and their interactions used in the multiple regression analysis.

Angler	**Physical**
Fishing method	Structure age
Boat length	Number of crossmembers
Engine horsepower	Number of legs
Presence of echosounder	Number of wells
Presence of LORAN	Water depth
Presence of graph recorder	Submerged surface area
	Volume of water enclosed
Geological	Structure manned
Mean sediment size	Structure in production
	Temporal/meteorological
	Linear date
	Quadratic date
	Cubic date
	Wind speed
Interactions	Wind direction
Boat length × Hp	Air temperature
Quadratic structure age	
Structure age × number of legs	
Structure age × number of crossmembers	
Structure age × submerged surface area	
Number of legs × number of cross members	
Number of legs × number of wells	
Number of legs × enclosed volume	
Number of legs × submerged surface area	
Structure manned × structure in production	
Water depth × volume of water enclosed	
Water depth × submerged surface area	
Submerged surface area × volume of water	

Results

A total of 55 anglers and 10 charterboat operators returned logbooks with usable information, a 45.8% and 43.5% return rate, respectively. The participants fished at 467 different oil and gas platforms a total of 1196 separate times. Anglers fished at platforms on 666 occasions and caught a total of 20,559 fish representing over 46 different species (Table 2). Charterboat operators fished at platforms 530 times and caught a total of 16,280 fish representing over 42 different species (Table 2).

A five-factor PCA explained 45.7% of the variance of the original data set and allowed us to reduce the data from the 17 separate species or species groups into a smaller data set of presumably related species (Table 3). The first factor was defined as a reef fish factor which included high positive loadings for greater amberjack, grey triggerfish, grouper, other snapper and red snapper, and a negative loading for spotted seatrout (Table 3). The pelagic fish factor consisted of positive loadings for dolphin, king mackerel, little tunny and Spanish mackerel, and a negative loading for silver/sand seatrout (Table 3). The third factor was composed of high positive loadings of Atlantic croaker and silver/sand seatrout (Table 3). The fourth factor was composed of high positive loadings of bluefish and red drum (Table 3). The fifth consisted of positive loadings for cobia and sharks, and a high negative loading for blue runner (Table 3). The strongest ecological relationships within a PC existed for reef fish and pelagic fish PC's. These groupings included species with similar life histories, habits, and abundances. The biological relationships between the species in the other PC's were more tenuous; however they did provide information on factors relating to the species relative abundance.

Results of the MRA of ln(CPUE + 1) of spotted seatrout with the predictor variables indicated spotted seatrout abundances were highest near small, nonproducing structures in shallow water. Fourteen

Table 2

Composition of catch around oil and gas platforms of angler and charterboat operator logbook participants, March 1987–March 1988.

	Angler		Charterboat operator	
Species/Group	No. caught	Percent	No. caught	Percent
Atlantic croaker (*Micropogonias undulatus*)	385	1.9	327	2.0
Atlantic spadefish (*Chaetodipterus faber*)	16	0.1	3	0.0
Bearded brotula (*Brotula barbata*)	14	0.1	—	—
Black drum (*Pogonias cromis*)	118	0.6	8	0.0
Blackfin tuna (*Thunnus atlanticus*)	20	0.1	5	0.0
Bluefish (*Pomatomus saltatrix*)	699	3.4	460	2.8
Blue marlin (*Makaira nigricans*)	2	0.0	2	0.0
Blue runner (*Caranx fusus*)	209	1.0	70	0.4
Cobia (*Rachycentron canadum*)	216	1.1	203	1.2
Crevalle jack (*Caranx hippos*)	41	0.2	19	0.1
Cubbyu (*Equetus umbrosus*)	5	0.0	—	—
Dolphin (*Coryphaena hippurus*)	209	1.0	172	1.1
Florida pompano (*Trachinotus carolinus*)	5	0.0	324	2.0
Flounder (*Paralichthys* sp.)	1	0.0	7	0.0
Gafftopsail catfish (*Bagre marinus*)	56	0.3	17	0.1
Great barracuda (*Sphyraena barracuda*)	19	0.1	27	0.2
Greater amberjack (*Seriola dumerili*)	625	3.0	1086	6.7
Grey triggerfish (*Balistes capriscus*)	635	3.1	211	1.3
Grouper (Family: Serranidae)	422	2.1	583	3.6
Grunts (*Haemulon* sp.)	44	0.2	5	0.0
Hake (*Urophycis* sp.)	1	0.0	2	0.0
Hardhead catfish (*Arius felis*)	301	1.5	133	0.8
King mackerel (*Scomberomorus cavalla*)	198	1.0	292	1.8
Ladyfish (*Elops saurus*)	20	0.1	3	0.0
Little tunny (*Euthynnus alletteratus*)	183	0.9	147	0.9
Lookdown (*Selene vomer*)	9	0.0	—	—
Other jacks (*Caranx* sp.)	49	0.2	14	0.1
Other snapper (Family: Lutjanidae)	443	2.2	809	5.0
Pinfish (*Lagodon rhomboides*)	66	0.3	70	0.4
Puffer (Family: Tetraodontidae)	1	0.0	—	—
Rainbow runner (*Elagatis bipinnulata*)	1	0.0	—	—
Rays (Family: Dasyatidae)	1	0.0	1	0.0
Red drum (*Sciaenops ocellatus*)	622	3.0	637	3.9
Red snapper (*Lutjanus campechanus*)	7315	35.6	3977	24.4
Sharks (Order: Selachii)	165	0.8	236	1.4
Sheepshead (*Archosargus probatocephalus*)	31	0.2	4	0.0
Shrimp eel (*Ophichthus* sp.)	—	—	10	0.1
Silver/sand seatrout (*Cynoscion* sp.)	1716	8.3	1407	8.6
Skipjack tuna (*Euthynnus pelamis*)	3	0.0	157	1.0
Spanish mackerel (*Scomberomorus maculatus*)	484	2.4	211	1.3
Spotted seatrout (*Cynoscion nebulosus*)	5108	24.8	4605	28.3
Squirrelfish (*Holocentrus* sp.)	—	—	12	0.1
Tarpon (*Megalops atlanticus*)	3	0.0	1	0.0
Tripletail (*Lobotes surinamensis*)	65	0.3	7	0.0
Wahoo (*Acanthocybium solanderi*)	19	0.1	10	0.1
White spotted soapfish (*Rypticus maculatus*)	9	0.0	—	—
Yellowfin tuna (*Thunnus albacares*)	5	0.0	—	—
Total	20,559		16,280	

significant predictor variables explained 42.2% of the variance contained in spotted seatrout ln(CPUE + 1) (Table 4). Water depth had the highest partial correlation coefficient (r^2) and a negative regression coefficient (Table 4), indicating that spotted seatrout were more prevalent in shallow water. Regression coefficients were negative for submerged surface area × volume of water enclosed, submerged surface area,

Table 3

Common factor analysis using principal component analysis for the first five factors of ln(CPUE + 1) for the 17 most frequently caught species by logbook participants, March 1987–March 1988. Loadings below 0.35 are marked with a dash.

	Principal component				
Species/Group	Reef fish	Pelagic fish	Atlantic croaker Silver/sand seatrout	Bluefish Red drum	Cobia Bluerunner Shark
Atlantic croaker	—	—	0.755	—	—
Bluefish	—	—	—	0.766	—
Bluerunner	—	—	—	—	−0.681
Cobia	—	—	—	—	0.379
Dolphin	—	0.406	—	—	—
Greater amberjack	0.664	—	—	—	—
Grey triggerfish	0.515	—	—	—	—
Grouper	0.691	—	—	—	—
King mackerel	—	0.636	—	—	—
Little tunny	—	0.600	—	—	—
Other snapper	0.582	—	—	—	—
Red drum	—	—	—	0.589	—
Red snapper	0.613	—	—	—	—
Sharks	—	—	—	—	0.350
Silver/sand seatrout	—	−0.401	0.671	—	—
Spanish mackerel	—	0.600	—	—	—
Spotted seatrout	−0.474	—	—	—	—
Eigenvalue	2.248	1.691	1.448	1.235	1.141
Proportion of variance explained	0.134	0.103	0.082	0.073	0.065
Cumulative variance explained	0.134	0.236	0.319	0.392	0.457

Table 4

Significant variables of a multiple regression of spotted seatrout ln(CPUE + 1) from logbook participants, March 1987–March 1988, based on physical, temporal, geological, meteorological, and angler characteristic variables and their interactions.

Variable	b value	Partial r^2
Water depth	−0.03	0.230
Surface area × volume	-1.1×10^{-8}	0.168
Water depth × volume	1.6×10^{-7}	0.162
Water depth × surface area	2.2×10^{-6}	0.132
Number of legs	0.01	0.060
Surface area	-5.7×10^{-5}	0.038
Echosounder presence	−0.21	0.037
Fishing method	−0.26	0.033
Quadratic data	−0.01	0.025
Boat length	0.08	0.017
LORAN presence	−0.17	0.012
Engine horsepower	-7.2×10^{-4}	0.008
Structure in production	−0.14	0.006
Number of legs × wells	-2.7×10^{-4}	0.006
Number of wells	—	N.S.
Volume	—	N.S.
Intercept	0.93	
Model r^2	0.42	

N.S. = not significant at the 1% level.

number of legs × number of wells, and whether the structure was in production; and coefficients were positive for the number of legs, water depth × submerged surface area, and water depth × volume of water enclosed. Since the regression coefficients were negative for water depth, fishing method, quadratic date, boat horsepower, and the presence of LORAN and echosounder, catch rates of spotted seatrout were highest while bottom-fishing by relatively small vessels without sophisticated electronics. Based on the plot of the sum of the linear and quadratic components of month, spotted seatrout were most abundant in the late spring and early summer (Fig. 1).

Multiple-regression analysis suggested reef fish were most abundant near large complex structures at intermediate water depths (Fig. 2). Ten significant predictor variables accounted for 35.2% of the variance in the reef fish factor (Table 5). The regression coefficients of water depth, volume of water enclosed, and the interactions of submerged surface area × volume of water enclosed, and the number of legs × number of crossmembers were positive, while negative regression coefficients were observed of the interactions of water depth × volume of water enclosed, and water

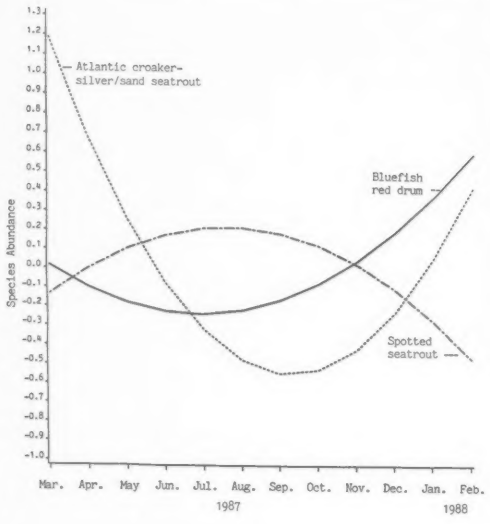


Figure 1

Calculated values of Atlantic croaker–silver/sand seatrout, bluefish–red drum, and spotted seatrout abundance on orthogonal of month from multiple regressions.

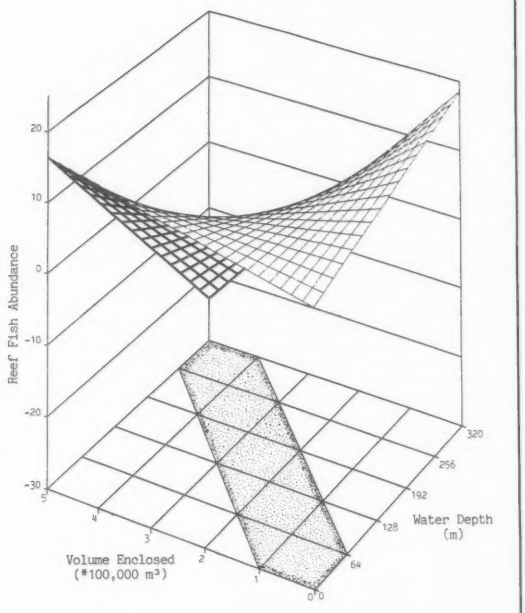


Figure 2

Response surface plot of water depth, volume of water enclosed by oil and gas platforms, and reef fish abundance from the multiple regression of principal component scores for catch data from logbook participants. Note: stippled area represents realistic values of volume of water enclosed at various depths for oil and gas platforms.

depth × submerged surface area (Table 5). Platform age did not affect the abundance of reef fish as evidenced by the negative regression coefficient for quadratic age of the platform (Table 5). Angler characteristics were not good predictors of reef fish catches, with only the presence of graph recorders and fishing method being significant (Table 5). Since the regression coefficient of fishing method was negative, reef fish catches were highest while bottom fishing.

Catches of pelagic fish were higher while trolling in relatively small, well-equipped vessels near large unmanned structures in intermediate water depths (Fig. 3). Retention of 10 significant predictor variables accounted for 31.5% of variance in the pelagic fish factor (Table 5). Regression coefficients for fishing method, LORAN presence, linear date, submerged surface area, water depth, and the interaction of submerged surface area and volume of water enclosed were positive from the MRA, while negative regression coefficients were found for the interactions of structure manned × structure in production, water depth × submerged surface area, and water depth × volume of water enclosed and boat length (Table 5).

Highest abundances of Atlantic croaker and silver/sand seatrout were found near small, manned platforms in deep water. Angler characteristic variables had little influence on their catch rates. Eight significant predictor variables explained 18.4% of the Atlantic croaker–silver/sand seatrout factor (Table 5). Temporal variables (quadratic date and linear date) had the highest partial r^2 values (Table 5) and indicated Atlantic croaker–silver/sand seatrout were most abundant in the early spring (Fig. 1). Positive regression coefficients were found for water depth and the interaction of structure manned × structure in production, and negative regression coefficients were found for volume of water enclosed and structure age × submerged surface area. LORAN presence and fishing method were the only significant angler characteristic variables retained in MRA (Table 5).

Based on MRA results, highest catches of bluefish and red drum occurred while trolling from late winter to early spring near platforms with complex construction. Retention of five significant predictor variables explained 14.5% of the variance in the bluefish–red drum factor (Table 5). The positive regression coefficient and the high partial r^2 (Table 5) for the interac-

Table 5

Significant variables of multiple regressions of reef fish, pelagic fish, Atlantic croaker–silver/sand seatrout, bluefish–red drum, and blue runner–shark–cobia principal-component scores from logbook participants, March 1987–March 1988, based on physical, temporal, geological, meteorological, and angler characteristic variables and their interactions.

	Reef fish		Pelagic fish		Atlantic croaker–silver/sand seatrout		Bluefish–red drum		Blue runner–shark–cobia	
Variables	b value	Partial r^2	b value	Partial r^2	b value	Partial r^2	b value	Partial r^2	b value	Partial r^2
Water depth	0.04	0.17	0.02	0.03	0.01	0.01	—	—	−0.01	0.04
Surface area × volume	1.6×10^{-9}	0.12	1.1×10^{-9}	0.05	—	—	—	—	—	—
Water depth × volume	-3.2×10^{-7}	0.08	-1.1×10^{-7}	0.04	—	—	—	—	—	—
Water depth × surface area	-2.3×10^{-6}	0.06	-1.8×10^{-6}	0.04	—	—	—	—	—	—
Number of legs	−0.01	0.01	−0.01	0.04	—	—	—	—	—	—
Surface area	—	—	5.5×10^{-5}	0.02	—	—	—	—	2.4×10^{-5}	0.02
Echosounder	—	—	—	—	—	—	−0.19	0.01	−0.21	0.01
Fishing method	−0.51	0.06	1.13	0.20	0.35	0.02	0.45	0.04	−0.39	0.03
Quadratic date	—	—	—	—	0.02	0.08	0.01	0.01	—	—
Boat length	—	—	−0.07	0.03	—	—	—	—	—	—
LORAN presence	—	—	0.43	0.04	−0.33	0.02	—	—	—	—
Number of legs × crossmembers	2.5×10^{-5}	0.02	—	—	—	—	1.9×10^{-5}	0.08	—	—
Graph recorder	−0.23	0.02	—	—	—	—	0.23	0.01	0.17	0.01
Quadratic age of platform	-2.8×10^{-6}	0.01	—	—	—	—	—	—	—	—
Volume	1.8×10^{-5}	0.01	—	—	-3.5×10^{-6}	0.01	—	—	—	—
Linear date	—	—	0.04	0.03	0.04	0.03	—	—	−0.02	0.01
Structure manned × production	—	—	−0.14	0.01	0.11	0.01	—	—	—	—
Age × surface area	—	—	—	—	-2.4×10^{-7}	0.01	—	—	—	—
Intercept	−0.51		−0.11		−0.11		0.45		0.31	
Model r^2	0.35		0.32		0.18		0.15		0.12	

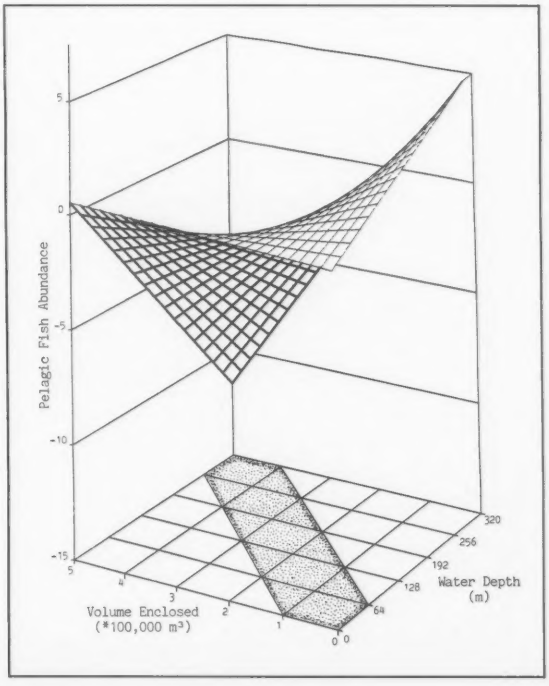


Figure 3

Response surface plot of water depth, volume of water enclosed by oil and gas platforms, and pelagic fish abundance from the multiple regression of principal component scores for catch data from logbook participants. Note: stippled area represents realistic values of volume of water enclosed at various depths for oil and gas platforms.

tion of the number of legs × number of crossmembers indicated that bluefish and red drum were most abundant near platforms with complex construction. Based on the plot of the orthogonal components of month, bluefish and red drum catch rates were highest in the early spring and late winter (Fig. 1). A positive regression coefficient for fishing method and negative regression coefficients for the presence of echosounders and graph recorders (Table 5) indicated that highest catches of bluefish and red drum occurred while trolling and that sophisticated electronic equipment did not increase catch rates.

Shark and cobia catches were highest while bottom fishing in the spring near large platforms in shallow water. The MRA with six significant predictor variables accounted for 11.5% of the variance in the shark–cobia factor (Table 5). The negative regression coefficient for water depth and positive regression coefficient for submerged surface area (Table 5) provide evidence that shark and cobia abundances were highest in shallow waters near large structures. Highest catches of shark and cobia occurred while bottom fishing in the spring, based on the negative regression coefficient for fishing method and linear date (Table 5). Conflicting results on the presence of electronic gear were found with a positive regression coefficient for presence of graph recorders and a negative regression coefficient for the presence of echo sounders (Table 5).

Discussion

Anglers and charterboat operators utilized the entire range of sizes and operational types of platforms available off the coast of Louisiana (single-well caissons, steel template platforms, and mobile semisubmersible drilling platforms), although certain trends in platform size utilization and fishing method were evident. Nearshore fishermen most often fished at the small structures (i.e., caissons) in shallow water (i.e., <10 m), while offshore bottom-fishing and trolling fishermen fished near much larger steel template platforms in deeper water (i.e., >30 m). Charterboat operators had larger vessels and were able to fish in deeper waters and farther offshore than anglers.

Anglers and charterboat operators caught a total of 36,839 fish representing at least 46 different species, providing evidence for the high diversity of fish around the oil and gas platforms. Fishes caught ranged from relatively common and highly desirable species such as spotted seatrout and red snapper to relatively rare fishes such as hake, bearded brotula, and squirrel fish. Highly sought-after gamefish such as tarpon, blue marlin, king mackerel, and yellowfin tuna were also caught. Catches by angling are selective and biased towards larger species because of the hook-and-line gear utilized, and usually only carnivorous species are susceptible to the gear. Consequently species not susceptible to angling were not represented (Grimes et al. 1982).

The associations of fish identified by the reef fish and pelagic fish PC's were in agreement with fish classification systems using direct observation around natural and artificial reefs in the Gulf of Mexico by Starck (1968) and Lukens (1981). This confirms that these groupings have an ecological basis, and were not an artifact of the sampling or analysis techniques.

Factors affecting the abundances of fish

Physical platform variables Generally, the highest abundances of spotted seatrout were found in shallow water (i.e., <10 m) around small, non-producing platforms such as caissons. These results were expected, as this estuarine-dependent species (Johnson and Seaman 1982) would likely have its highest abundances in shallow water near estuaries.

Our results suggest that reef fish, Atlantic croaker, and silver/sand seatrout abundances increased with size and complexity of the artificial reef, agreeing with past studies (Turner et al. 1969, Grove and Sonu 1983). However, an optimal artificial reef size occurred for reef fish based on the response surface plot of water depth, volume enclosed, and fish abundance as highest reef-fish abundances occurred at intermediate depths (i.e., 70–100 m) near relatively large platforms (i.e., mean volume enclosed 150,000–250,000 m^3). The optimal size range of oil and gas platforms acting as artificial reefs was significantly larger than the optimal artificial reef sizes reported in past studies. This difference could be due to the open construction and lack of interstitial spaces on oil and gas platforms which may not be as efficient at attracting or increasing secondary production of fish as the large rubble or prefabricated artificial reef units on which past estimates were calculated. Also, oil and gas platforms extend throughout the entire water column, and because many reef fish are demersal, a large portion of the platform may not be suitable reef-fish habitat. Reef-fish abundances were lowest at the largest platforms in extremely deep water, probably because the water depths exceeded the preferred ranges for these species.

Physical platform variables were not important predictor variables of pelagic fish abundance. Our results are consistent with Wickham et al. (1973) and Grove and Sonu (1983) who concluded that pelagic fishes respond to the visual attraction of artificial reefs and not to the overall size or surface area.

Bluefish, red drum, cobia, and shark abundances were highest around large, structurally complex platforms. These species were probably not trophically dependent on the structures, but were attracted to platforms by an optical stimulus as reported by Wickham et al. (1973) for cobia.

Age of the structure was not a significant factor in explaining fish composition or abundance around oil and gas platforms. Therefore it appears that the species-equilibrium model, which suggests that the number of species present and their abundances increase rapidly over a colonization period eventually stabilizing (MacArthur and Wilson 1967), was not applicable, or that the platforms may have been fully

colonized at the start of the study and we were sampling after species stabilization occurred. The latter explanation seems most likely, because the age of platforms in our study ranged from 8 months to 30 years, and full colonization of artificial reefs in the northern Gulf of Mexico can occur in as little as 15 months (Lukens 1981).

Seasonal variation Season was an important factor affecting the abundances of fish around oil and gas platforms. Smith (1979) and Lukens (1981) reported large fluctuations in species composition and abundance around natural and artificial reefs in the northern Gulf of Mexico, and based on our results this would include fish populations around oil and gas platforms off the Louisiana coast.

The apparent higher abundances of spotted seatrout in the spring and summer may be a result of a temperature-induced increase in feeding rate and/or the aggregation of the fish into spawning schools (Johnson and Seaman 1982).

The increase in pelagic fish catches from winter through fall indicated that abundance may have been related to water temperature. This is consistent with the findings by Fable et al. (1981), as they found that the charterboat catches of king mackerel and other pelagic species in the northeast Gulf of Mexico increased with water temperature.

Lassuy (1983) reported that Atlantic croaker abundance was highest in the spring and summer, while Sutter and McIlwain (1982) reported silver/sand seatrout abundance to be highest in the winter and spring. This may explain the apparent conflicts in the results from the MRA with respect to seasonal abundances of these two species. Silver/sand seatrout may have been abundant in the winter and spring, and Atlantic croaker in the spring and summer. However, when these species were grouped the seasonal abundance results explained only silver/sand seatrout and not the entire group.

Our results, along with those of others (Gallaway et al. 1981b, Reagan 1982) provided evidence that bluefish and red drum were seasonal transients with highest abundances from fall through spring. Shark and cobia abundances appeared to be highest in the spring and decreased thereafter.

Angler characteristic variables Overall, fishing power was not equal because fishermen with larger vessels and engines had access to deeper water, and fishermen with sophisticated electronics could more easily locate fish. Because reef fish, Atlantic croaker, and silver/sand seatrout are found in deep water, anglers with large vessels and engines had the highest catches for these species, while cobia, sharks, and pelagic species were more frequently caught by vessels having sophisticated electronics. Since spotted seatrout were found in shallow water, large vessels or sophisticated electronics did not increase spotted seatrout catches.

Geological and meteorological variables Geological and meteorological variables were not significant predictors of fish abundance around oil and gas platforms. Meteorological variables were probably not important because fishermen generally fish only in good weather, consequently catch rates during poor weather conditions were not reported.

Conclusions

The physical construction of oil and gas platforms precludes sampling of the associated sportfish populations using traditional methods (e.g., gillnets, trawls). Based on the results of this logbook program, the collection of CPUE data over long periods of time may be an effective technique of monitoring the fish populations susceptible to angling associated with artificial reefs. Although the data supplied by the logbooks is an index of relative abundance of fish susceptible to angling and is biased towards larger individuals, it provides a valuable source of data which is otherwise difficult to obtain.

With the advent of the "Rigs to Reefs" initiative in Louisiana, biological criteria to determine where to locate retired oil and gas platforms as artificial reefs was needed. Information derived from this study suggests that optimal artificial reef configurations exist, but vary depending on the species. To effectively site artificial reefs for reef fish, Atlantic croaker, and silver/sand seatrout there should be large complex platforms at intermediate depths; for pelagic species artificial reef size is not a factor, although they should again be placed at intermediate depths. Optimal siting of artificial reefs for spotted seatrout should include small structures in shallow water. Gallaway and Lewbel (1982) suggested that abundances of some species were directly proportional to the submerged surface area of oil and gas platforms. We believe that the relationship between fish abundances and artificial reefs is much more complex, with other factors, such as natural and temporal variability of species distribution and abundance interacting with physical platform variables and water depth to determine overall species abundances.

Acknowledgments

The authors thank the 55 anglers and 10 charterboat operators for maintaining logbooks; the oil and gas operators for providing information and drawings on

the platforms; Mr. Villere Reggio, Minerals Management Service, for additional platform information; Louisiana State Climatology Office for meteorological data; Drs. James Geaghan and Gary Shaffer for statistical assistance; Dr. Linda Jones and two anonymous reviewers for critical review of the manuscript and improving its contents. This study was part of a Master's thesis by David R. Stanley and was supported by the Department of Marine Sciences, LSU; the Louisiana Artificial Reef Initiative; and Dupont Inc. Educational Aid Program.

Citations

Bohnsack, J.A.
1989 Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bull. Mar. Sci. 44:631–645.

Bohnsack, J.A., and D.L. Sutherland
1985 Artificial reef research: A review with recommendations for future priorities. Bull. Mar. Sci. 37:11–39.

Chandler, C.R., R.M. Sanders Jr., and A.M. Landry Jr.
1985 Effects of three substrate variables on two artificial reef communities. Bull. Mar. Sci. 37:129–142.

Chatfield, C., and A.J. Collins
1980 Introduction to multivariate analysis. Chapman and Hall, NY, 246 p.

Coleman, E.
1984 Coastal Louisiana: climate and recreation. Sea Grant Coll. Prog., La. State Univ., Baton Rouge, 24 p.

Coleman, J.M., H.H. Roberts, and T.F. Moslow
1986 Sedentary sequences and seismic responses related to sea level change: Louisiana continental shelf. Report to Gulf of Mexico Research Consortium. School of Geoscience, La. State Univ., Baton Rouge, 96 p.

Continental Shelf Associates, Inc.
1982 Study of the effect of oil and gas activities on reef fish populations in the Gulf of Mexico OCS area. OCS Rep./MMS82-010, U.S. Dep. Inter., Minerals Manage. Serv., Gulf of Mexico OCS Reg., New Orleans, 210 p.

Demory, R.L., and J.T. Golden
1983 Sampling the commercial catch. *In* Nielson, L.A., and D.L. Johnson (eds.), Fisheries techniques, p. 421–430. Am. Fish. Soc., Bethesda, MD.

Dillon, W.R., and M. Goldstein
1984 Multivariate analysis. John Wiley, NY, 587 p.

Fable, W.A. Jr., H.A. Brusher, L. Trent, and J. Finnegan Jr.
1981 Possible temperature effects on charter boat catches of king mackerel and other coastal pelagic species in northwest Florida. Mar. Fish. Rev. 43(8):21–26.

Gallaway, B.J.
1984. Assessment of platform effects on snapper populations and fisheries. *In* Proc., Fifth annual Gulf of Mexico information transfer meeting, New Orleans, Nov. 27–29, 1984, p. 130–137. OCS Study/MMS85-0008, U.S. Dep. Inter., Minerals Manage. Serv., Metarie, LA.

Gallaway, B.J., and G.S. Lewbel
1982 The ecology of petroleum platforms in the northwestern Gulf of Mexico: A community profile. Open-file Rep. 82-03, U.S. Fish Wildl. Serv., Office Biol. Serv., Wash. DC, 91 p.

Gallaway, B.J., L.R. Martin, R.L. Howard, G.S. Boland, and G.D. Dennis
1981a Effects on artificial reef and demersal fish and macrocrustacean communities. *In* Middleditch, B.S. (ed.), Environmental effects of offshore oil production: The Buccaneer gas and oil field study, p. 237–299. Mar. Sci. Vol. 14, Plenum Press, NY.

Gallaway, B.J., M.F. Johnson, L.R. Martin, F.J. Margraf, G.S. Lewbel, R.L. Howard, and G.S. Boland
1981b The artificial reef studies, Vol. 2. *In* Bedinger Jr., C.A., and L.Z. Kirby (eds.), Ecological investigations of petroleum production platforms in the central Gulf of Mexico. SWRI Proj. 01-5245, U.S. Dep. Inter., Bur. Land Manage., Gulf of Mexico OCS Reg., New Orleans, 199 p.

Gooding, R.M., and J.J. Magnuson
1967 Ecological significance of a drifting object to pelagic fishes. Pac. Sci. 2:486–497.

Grimes, C.B., C.S. Manooch, and G.R. Huntsman
1982 Rock and reef outcropping fishes of the outer continental shelf of North Carolina and South Carolina and ecological notes on red porgy and vermillion snapper. Bull. Mar. Sci. 32:277–289.

Grove, R.S., and C.J. Sonu
1983 Review of Japanese fishing reef technology. Tech. Rep. 83-RD-137, South. Calif. Edison Co., Rosemead, CA, 112 p.

Gunter, G.
1963 The fertile fisheries crescent. J. Miss. Acad. Sci. 9: 286–290.

Hastings, R.W., L.H. Ogren, and M.T. Mabry
1976 Observations on the fish fauna associated with offshore platforms in the Northeastern Gulf of Mexico. Fish. Bull., U.S. 74:387–401.

Hunter, J.R., and C.T. Mitchell
1967 Association of fishes with flotsam in the offshore waters of Central America. Fish. Bull., U.S. 66:13–29.
1968 Field experiments on the attraction of pelagic fish to floating objects. J. Cons. Perm. Explor. Mer 31:427–434.

Huntsman, G.R.
1981 Ecological considerations influencing the management of reef fishes. *In* Aska, D.Y. (ed.), Artificial reefs: Conference proceedings, p. 167–175. Rep. 41, Fla. Sea Grant Coll. Prog., Univ. Fla., Gainesville.

Johnson, D.R., and W. Seaman Jr.
1982 Species profiles: Life history requirements and environmental requirements of coastal fishes and invertebrates—spotted seatrout. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.43), 18 p.

Klima, E.F., and D.A. Wickham
1971 Attraction of coastal pelagic fishes with artificial structures. Trans. Am. Fish. Soc. 100:86–99.

Lassuy, D.R.
1983 Species profiles: Life history requirements and environmental requirements (Gulf of Mexico)—Atlantic croaker. U.S. Fish Wildl. Serv. FWS/OBS-82/11.3, 12 p.

Luckhurst, B.E., and K. Luckhurst
1978 Analysis of the influence of substrate variables on coral reef fish communities. Mar. Biol. (Berl.) 49:317–323.

Lukens, R.R.
1981 Ichthyofaunal colonization of a new artificial reef in the northern Gulf of Mexico. Gulf Res. Rep. 7:41–49.

MacArthur, R.H., and E.O. Wilson
1967 The theory of island biogeography. Princeton Univ. Press, Princeton, NJ, 203 p.

Molles, M.C. Jr.
1978 Fish species diversity on model and natural reef patches: Experimental insular biogeography. Ecol. Monogr. 48: 289–305.

Moore, D., H.A. Brusher, and L. Trent
1970 Relative abundance, seasonal distributions and species composition of demersal fishes off Louisiana and Texas, 1962–1964. Contrib. Mar. Sci. 15:45–70.

Ogawa, Y.
1982 The present status and future prospects of artificial reefs: Developmental trends of artificial reef units. *In* Vik, S.F. (ed.), Japanese artificial reef technology, p. 23–41. Tech. Rep. 604, Aquabio, Inc., Bellair Bluffs, FL.

Pennington, M.
1983 Efficient estimators of abundance for fish and plankton. Biometrics 39:281–286.
1985 Estimating the relative abundance of fish from a series of trawl surveys. Biometrics 41:197–202.

Reagan R.E.
1982 Species profiles: Life history requirements and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico)—red drum. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.36), 18 p.

Reggio, V.C. Jr.
1987 Rigs-to-reefs: The use of obsolete petroleum structures as artificial reefs. OCS Rep./MMS87-0015, U.S. Dep. Inter., Minerals Manage. Serv., Gulf of Mexico OCS Reg., New Orleans, 17 p.

Rousenfell, G.A.
1972 Ecological effects of offshore construction. J. Mar. Sci. 2:1–208.

SAS Institute Incorporated
1985 SAS user's guide: Statistics, version 5 edition. SAS Inst., Cary, NC, 956 p.

Smith, G.B.
1979 Relationship of eastern Gulf of Mexico reef fish communities to species equilibrium theory of insular biogeography. J. Biogeogr. 6:49–61.

Sonnier, F., J. Teerling, and H.D. Hoese
1976 Observations on the offshore reef and platform fish fauna of Louisiana. Copeia 1976:105–111.

Starck, W.A.
1968 A list of fishes of Alligator reef, Florida with comments on the nature of Florida reef fish fauna. Undersea Biol. 1: 5–40.

Stephens, J.S. Jr., and K.E. Zerba
1981 Factors affecting fish diversity on a temperate reef. Environ. Biol. Fishes 6:111–121.

Stone, R.B., H.L. Pratt, R.O. Parker Jr., and G.E. Davis
1979 A comparison of fish populations on an artificial and natural reef in the Florida Keys. Mar. Fish. Rev. 41:1–11.

Sutter, F.C., and T.D. McIlwain
1982 Species profiles: Life history requirements and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico)—sand seatrout and silver seatrout. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.36), 16 p.

Sztramko, L.
1986 Lake Erie angler diary program. 1985. Lake Erie Fish. Assess. Unit Rep. 1986-4. Ontario Minist. Nat. Resourc., Wheatley, Ontario, 45 p.

Turner, C.F., E.E. Ebert, and R.R. Given
1969 Man-made reef ecology. Calif. Dep. Fish Game, Fish. Bull. 146, 221 p.

Vik, S.F. (editor)
1982 Japanese artificial reef technology. Tech. Rep. 604, Aquabio, Inc, Bellair Bluffs, FL, 380 p.

Wickham, D.A., J.W. Watson, and L.H. Ogren
1973 The efficacy of midwater artificial structures for attracting pelagic sport fish. Trans. Am. Fish. Soc. 102:563–572.

Witzig, J.
1986 Fishing in the Gulf of Mexico 1984 marine recreational fishing results. *In* Proceedings, Sixth annual Gulf of Mexico information transfer meeting, New Orleans, p. 103–105. OCS Study MMS86-0073, U.S. Dep. Inter., Minerals Manage. Serv., Gulf of Mexico OCS Reg., New Orleans.

Abstract.—Serum progesterone and testosterone levels, as measured by radioimmunoassay, were used to estimate the mean length at attainment of sexual maturity (LSM) in a sample of 124 female and 31 male incidentally-killed Dall's porpoises *Phocoenoides dalli*. Females with serum progesterone levels greater than 1.34 ng/mL were considered mature. The LSM for females was estimated at 169.0 cm using Kasuya's "summation" technique. A technique to fit a two-phase regression model to the male data produced an estimated LSM for males of 183.0 cm. Overall, the estimates for the LSM in this study agreed well with previously published reports using histological and morphological measures of sexual maturity. Hormonal estimation of maturity is proposed as a rapid, inexpensive, and potentially non-lethal alternative technique in odontocete populations.

Manuscript accepted 17 October 1990.
Fishery Bulletin, U.S. 89:161–165 (1991).

Use of Serum Progesterone and Testosterone to Estimate Sexual Maturity in Dall's Porpoise *Phocoenoides dalli*

Jonathan L. Temte

Hatfield Marine Science Center, Oregon State University, Newport Oregon 97365
Present address: Department of Zoology, University of Wisconsin
Madison, Wisconsin 53706

Estimation of the mean age and length at the attainment of sexual maturity in odontocetes has traditionally relied upon morphological or histological parameters, thus necessitating whole animal preparations. Examination of reproductive tissue allows for the determination of maturity. When this information is coupled with age/length data, the age or length at attainment of sexual maturity for females and males in a population can be determined using a variety of methods (DeMaster 1984). These methods, however, implicitly require the collection of dead marine mammals in the field.

Several authors have used radioimmunoassay (RIA) to assess reproductive condition in living odontocetes. For example, RIA of progesterone has been used as an indicator of luteal function in *Tursiops truncatus*, *Delphinus delphis* (Kirby and Ridgway 1984, Sawyer-Steffan et al. 1983), and *Stenella longirostris* (Wells 1984). Likewise, measurements of serum testosterone by RIA have been used to assess male sexual condition in *T. truncatus* (Harrison and Ridgway 1971) and *S. longirostris* (Wells 1984).

Temte and Spielvogel (1985) demonstrated that serum progesterone concentration, as measured by RIA, was a good predictor of corpus luteum mean diameter in a sample of 32 incidentally-killed pregnant or lactating Dall's porpoises *Phocoenoides dalli* from the northwestern North Pacific Ocean. Furthermore, they noted that 17 sexually immature females (no corpora present in ovaries) had very low concentrations of serum progesterone (Table 1).

In this study the results of progesterone and testosterone RIA in 124 female and 31 male Dall's porpoises, respectively, were used to estimate the mean length at attainment of sexual maturity (LSM) in this species. The results are compared to those obtained using traditional histological techniques to demonstrate the effectiveness of this inexpensive and nonlethal technique.

Methods

Blood samples

During June and July of 1982, personnel of the National Marine Mammal Laboratory (NMFS) obtained blood samples from a total of 105 Dall's porpoises that were incidentally-killed in Japanese salmon gillnets in the North Pacific Ocean. The following groups were represented in the sample: 21 non-pregnant, nonlactating females in which the maturity status was not known (149–199 cm, standard body length); 30 pregnant females (167–200 cm); 23 lactating females (167–200 cm), and 31 males in which the maturity status was not known (101–210 cm). Samples of whole blood were drawn and centrifuged using methods described

Table 1
Serum progesterone concentrations [P] in immature and mature female Dall's porpoises. Data from 1980 sample of Temte and Spielvogel (1985).

Status	No.	Mean [P] (ng/mL)	SD	Range of [P]
Mature	33	14.76	12.43	0.0–45.3
Pregnant (P)	24	19.40	11.31	0.9–45.3
Lactating (L)	8	2.63	3.75	0.0–11.4
non-P, non-L	1	0.49		
Immature*	17	0.27	0.46	0.0–1.3

*Excluding one immature female with a large follicle and 31.1 ng/mL progesterone.

by Temte and Spielvogel (1985). In these samples, however, serum was decanted into 1.5-mL plastic ultracentrifuge tubes and frozen at −20°C until assays were performed.

RIA for progesterone

Progesterone RIA was identical to that reported by Temte and Spielvogel (1985). This assay had previously been validated for porpoise serum, and chromatography had shown an absence of interference from other serum constituents. Triplicate volumes of porpoise serum (10 μL for pregnant, 50 μL for lactating, and 100 μL for non-pregnant, non-lactating females) were doubly extracted utilizing a 1:2 mixture of benzene and hexane (Sawyer-Steffan and Kirby 1980). The antiserum used was anti-progesterone-11-BSA, No. 1337 (Gordon D. Niswender). The intraassay coefficient of variation (COV) was 5.5%, while the interassay COV was 5.9%. The sensitivity of this assay was 0.1 ng/mL.

RIA for testosterone

The procedure for testosterone RIA was nearly identical to that for progesterone. Triplicate volumes of 25-μL porpoise serum were doubly extracted with 1:2 benzene:hexane. The antiserum used was anti-testosterone, No. s-250 (Gordon D. Niswender). The competitor was [^{3}H]testosterone (NET-553, New England Nuclear). The intraassay coefficient of variation (COV) was 6.3%, while interassay COV was 14.6%. The assay sensitivity was 0.3 ng/mL.

Maturity criteria for females

The mean serum progesterone for immature females reported in Temte and Spielvogel (1985) was 0.27 ng/mL. Assuming a normal distribution, 99% of immature females would be expected to have serum progesterone levels less than 1.34 ng/mL. Based upon this result, females with serum progesterone concentrations greater than 1.34 ng/mL were considered sexually mature. Whereas, this progesterone level is lower than the 3.0 ng/mL used by Kirby and Ridgway (1984) as an indicator of ovulation in *D. delphis* and *T. truncatus*, 94% of the immature females and 96% of the pregnant females reported in Temte and Spielvogel (1985) were correctly classified using this criteria.

Maturity criteria for males

Since samples were collected near the peak breeding period for Dall's porpoises (Newby 1982; see also Jefferson 1989), and considering the seasonal flux of testosterone in other odontocetes (Wells 1984), separation of immature and mature Dall's porpoises by testosterone level alone was theoretically possible in this study. Although Wells (1984) regarded serum testosterone concentrations of less than 8.0 ng/mL as baseline levels in *S. longirostris*, a natural break in the Dall's porpoise data occurred between 1.7 and 5.0 ng/mL. However, as tissue samples were not available for maturity assessment, no hormonal maturity criteria could be confirmed.

Estimation of LSM

The proportions of mature females in each 10-cm increment (135–225 cm) were calculated. Graphical analysis determined the length at which the cumulative probability of maturity, $\Sigma(m_i)$, equaled the cumulative probability of not being mature at that length or longer, $\Sigma(1-m_i)$. This method was first used by Kasuya (1972) and has been termed the summation technique by DeMaster (1984). It is recommended when small samples of size- or age-classes exist.

A small total sample precluded the use of the summation technique in males. As a consequence, a modification of the regression technique (see DeMaster 1984) was used to identify the LSM. Because testosterone concentrations demonstrated a discontinuity (see above), a continuous two-phase regression model (Yeager and Ultsch 1989; review by Nickerson et al. 1989) was used to objectively identify the transition point in the data. The transition point in the length represents the point at which the discontinuity occurred, or in this case, the LSM.

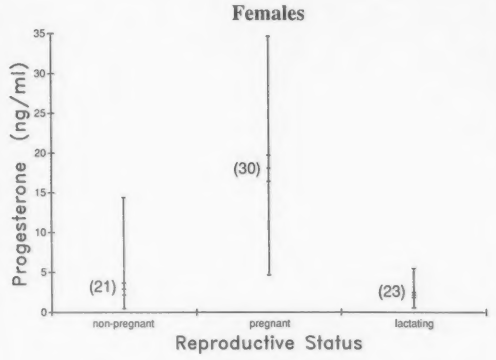


Figure 1
Serum progesterone concentrations for non-pregnant/non-lactating, pregnant, and lactating female Dall's porpoises. Vertical bars indicate ranges of values. Horizontal bars indicate means and standard errors. Sample sizes are in parentheses. Animals were collected June–July 1982 in the western North Pacific Ocean.

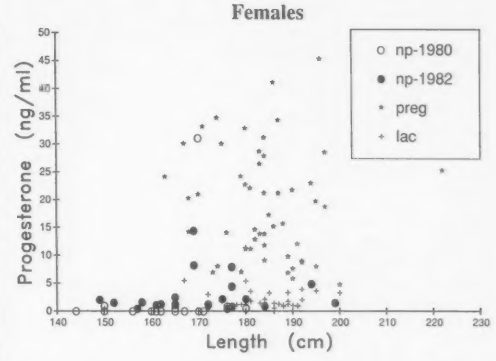


Figure 2
Serum progesterone concentration as a function of length in non-pregnant (1980 O; 1982 ●), pregnant (*), and lactating (+) female Dall's porpoises.

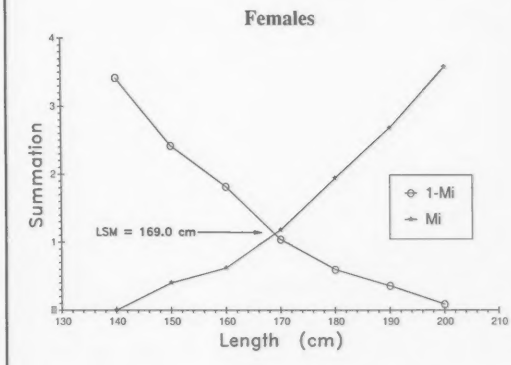


Figure 3
Summation technique for female Dall's porpoises based on progesterone values. Intersection of lines occurs when $\Sigma(m_i) = \Sigma(1-m_i)$.

Results

Comparison of 1982 and 1980 progesterone data

The results of the progesterone assays (1982 data: Fig. 1) were compared with results of Temte and Spielvogel (1985) (1980 data). No significant differences were found between the mean progesterone concentrations for pregnant females (1980: $n = 24$, $\bar{x} = 19.40$; 1982: $n = 30$, $\bar{x} = 18.09$; $P > 0.5$; Student's t-test), or for lactating females (1980: $n = 8$, $\bar{x} = 2.63$; 1982: $n = 23$, $\bar{x} = 2.17$; $P \gg 0.05$; Wilcoxson rank sum). Mean progesterone concentrations were significantly different for the two groups of non-pregnant, non-lactating porpoises (1980: $n = 19$, $\bar{x} = 1.91$; 1982: $n = 21$, $\bar{x} = 2.92$; $P < 0.01$; Wilcoxson rank sum). However, the mean length of the 1982 sample was significantly greater than that of the 1980 sample (1982: $\bar{x} = 171.2$ cm; 1980: $\bar{x} = 163.1$ cm; $P < 0.05$; Student's t-test), and the difference in mean progesterone could be due to a difference in the proportion of mature females. Therefore, the results of progesterone analysis in pregnant, lactating, and non-pregnant/non-lactating females from the 1982 sample were pooled with the results from the 1980 sample of Temte and Spielvogel (1985).

Females

Serum progesterone is plotted against length for 124 female Dall's porpoises (Fig. 2). The results demonstrate the incidence of high progesterone levels at lengths greater than 165 cm. These elevated levels were seen not only in pregnant females, but also in non-pregnant, non-lactating females, indicating possible ovulation. The summation technique provided an estimated LSM of 169.0 cm (Fig. 3).

Males

Serum testosterone displayed a marked increase with an increase in length. A natural break in the testosterone data occurred between 175 and 180 cm, when

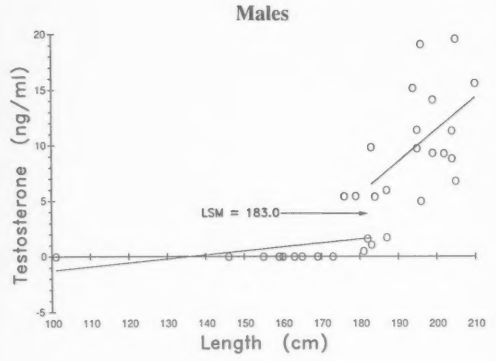


Figure 4
Serum testosterone concentration as a function of length for 31 male Dall's porpoises collected in 1982. Two-phase regression lines are shown.

testosterone increased from undetectable levels to relatively high levels. The best fitting two-phase regression model (Fig. 4) indicated that the transition point occurred at 183.0 cm. Hence, the LSM for males was estimated as 183.0 cm. The mean (± SE) testosterone concentration was 1.00 ± 0.52 ng/mL for males shorter than the LSM, and 10.46 ± 1.20 ng/mL for males longer than the LSM.

Discussion

Newby (1982), using the presence of ovarian scars and the 50th percentile method (see DeMaster 1984), estimated the LSM to be 170.5 cm for females in this western North Pacific population. The use of hormonal data alone provided a similar, but slightly lower, LSM estimate of 169.0 cm. However, based on the growth curves for females of this population (fig. 31 in Newby 1982), this 1.5-cm difference translates into small differences in ages.

The estimate for LSM in males of 183.0 cm is in very close agreement with the previously estimated LSM of 182.6 cm based on the 50th percentile method using testis-epididymal weight (Newby 1982). Direct comparison with previous studies are not possible due to the lack of variance estimates for LSM by the methods used. Nevertheless, the hormonal estimates of LSM provided in this study agree quite well with previous, non-hormonal methods.

Radioimmunoassay is a quick, economical, and accurate measure of reproductive condition. Small samples of blood (<1 mL) provide adequate serum for replicate assays. Previous studies have shown the high predictive value of serum progesterone level to corpus luteum size and reproductive state (Temte and Spielvogel 1985, Kirby and Ridgway 1984, Sawyer-Steffan et al. 1983). Moreover, such methods could allow the rapid collection of samples for maturity status assessment from large numbers of animals in the field.

Hormonal assessment of reproductive status may prove to be a non-lethal technique to estimate population parameters such as LSM. It is, at present, more applicable to captive animal studies. However, situations in which animals are killed incidentally may provide opportunities for obtaining concordant blood and reproductive tissue samples. Such sampling could allow the direct comparison of hormonal and histological methods of estimating maturity and establish appropriate hormonal criteria for future studies.

Seasonality in breeding may well limit the usefulness of this method in males (see Perrin and Donovan 1984) because testosterone undergoes seasonal fluctuation. In addition, the presence of environmental toxins may interfere with steroid hormone production. For example, Subramanian et al. (1987) have shown a significant negative relationship between testosterone concentration and DDE residue level.

There is potential for using progesterone, testosterone, and other hormonal parameters, such as chorionic gonadotropin, FSH, and LH, in the estimation of sexual maturity and reproductive status in marine mammal populations. As we expand our reproductive database in the cetacea, we also need to correlate histological and morphological states with hormonal parameters. Research protocols which include 10-mL samples of fresh blood and assessment of hormonal state should be encouraged.

Acknowledgments

I thank L.L. Jones, L.M. Tsunoda, and personnel of the National Marine Mammal Laboratory, NMFS, Seattle, Washington for collection of blood samples and exchange of information. F.L. Moore of Oregon State University Department of Zoology provided laboratory space for RIA. L.L. Jones and two anonymous reviewers made very helpful comments that greatly improved this manuscript. This study was made possible, in part, by support to the author from the Lutheran Brotherhood Medical Research Fund.

Citations

DeMaster, D.P.
1984 Review of techniques used to estimate the average age at attainment of sexual maturity in marine mammals. *In* Perrin, W.F., R.L. Brownell Jr., and D.P. DeMaster (eds.), Reproduction in whales, dolphins, and porpoises, p. 175–180. Rep. Int. Whaling Comm., Spec. Iss. 6, Cambridge.

Harrison, R.J., and S.H. Ridgway
1984 Gonadal activity in some bottlenose dolphins (*Tursiops truncatus*). J. Zool. (Lond.) 165:355–366.

Jefferson, T.A.
1989 Calving seasonality of Dall's porpoise in the eastern North Pacific. Mar. Mammal Sci. 5:193–195.

Kasuya, T.
1972 Growth and reproduction of *Stenella coeruleoalba* based on the age determination by means of dentinal growth layers. Sci. Rep. Whales Res. Inst., Tokyo 24:57–79.

Kirby, V.L., and S.H. Ridgway
1984 Hormonal evidence of spontaneous ovulation in captive dolphins, *Tursiops truncatus* and *Delphinus delphis*. *In* Perrin, W.F., R.L. Brownell Jr., and D.P. DeMaster (eds.), Reproduction in whales, dolphins, and porpoises, p. 459–464. Rep. Int. Whaling Comm., Spec. Iss. 6, Cambridge.

Newby, T.C.
1982 Life history of Dall's porpoise (*Phocoenoides dalli*, True 1885) incidentally taken by the Japanese high seas salmon mothership fishery in the northwestern North Pacific and western Bering Sea, 1978 to 1980. Ph.D. thesis, Univ. Wash., Seattle, 155 p.

Nickerson, D.M., D.E. Facey, and G.D. Grossman
1989 Estimating physiological thresholds with continuous two-phase regression. Physiol. Zool. 62:866–887.

Perrin, W.F., and G.P. Donovan
1984 Report of the workshop. *In* Perrin, W.F., R.L. Brownell Jr., and D.P. DeMaster (eds.), Reproduction in whales, dolphins, and porpoises, p. 1–24. Rep. Int. Whaling Comm., Spec. Iss. 6, Cambridge.

Sawyer-Steffan, J.E., and V. Kirby
1980 A study of serum steroid hormone levels in captive female bottlenose dolphins, their correlation with reproduction status, and their application to ovulation induction in captivity. U.S. Mar. Mammal Comm. Rep. MMC-77/22, 21 p.

Sawyer-Steffan, J.E., V. Kirby, and W.G. Gilmartin
1983 Progesterone and estrogen in the pregnant and nonpregnant dolphin, *Tursiops truncatus*, and the effects of induced ovulation. Biol. Reprod. 28:897–901.

Subramanian A., S. Tanabe, R. Tatsukawa, S. Saito, and N. Miyazaki
1987 Reduction of testosterone levels by PCBs and DDE in Dall's porpoises of northwestern North Pacific. Mar. Pollut. Bull. 18:643–646.

Temte J.L., and S. Spielvogel
1985 Serum progesterone and reproductive status of incidentally killed female Dall porpoises. J. Wildl. Manage. 49(1): 51–54.

Wells, R.S.
1984 Reproductive behavior and hormonal correlates in Hawaiian spinner dolphins, *Stenella longirostris*. *In* Perrin, W.F., R.L. Brownell Jr., and D.P. DeMaster (eds.), Reproduction in whales, dolphins, and porpoises, p. 465–472. Rep. Int. Whaling Comm., Spec. Iss. 6, Cambridge.

Yeager, D.P., and G.R. Ultsch
1989 Physiological regulation and conformation: A BASIC program for the determination of critical points. Physiol. Zool.62:888-907.

Detecting Differences in Fish Diets

David A. Somerton

Honolulu Laboratory, Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA, 2570 Dole Street
Honolulu, Hawaii 96822-2396

Statistical comparison of the diet of a predator between areas or time-periods allows one to distinguish true dietary differences from sampling variability and may lead to a better understanding of a species' feeding habits. Despite the utility of statistical testing, few procedures appropriate for dietary comparisons have been developed. Perhaps one impediment to the development of a general approach to dietary comparisons is the wide variety of ways in which diets have been expressed and the lack of consensus about which is best. For example, diets expressed as the numeric or gravimetric proportions of the total food consumed will require different approaches to statistical comparison than those expressed either as the proportion of the samples containing each of the various prey types, or as the index of relative importance of each prey type (Pinkas et al. 1971).

For cases in which diets are expressed in terms of gravimetric proportions, Crow (1979) and Ellison (1979) have recommended statistical tests of between-sample differences based on multivariate analysis of variance (MANOVA). Validity of such tests, however, requires that the prey proportions have a multivariate normal distribution and that the variance-covariance structure of the prey proportions is identical among samples (Morrison 1976). Recognizing that dietary data are unlikely to have these properties, Crow (1979) further recommended using MANOVA that incorporates non-parametric procedures. Herein, this recommendation is followed, and a new approach for testing differences in diets using non-parametric MANOVA is examined. This approach combines the usual measure of between-sample differences employed in parametric MANOVA (i.e., Hotelling's T^2 statistic; Morrison 1976) and a non-parametric procedure (i.e., a randomization test; Edgington 1987) to determine the significance of T^2. The method is then applied to determine whether the diet of pelagic armorhead *Pseudopentaceros wheeleri* from the Southeast Hancock Seamount changed between two sampling periods.

Materials and methods

Testing for between-sample differences is accomplished in three steps: (1) calculating for each sample the gravimetric dietary proportions and their variances and covariances, (2) calculating a measure of the statistical difference between samples, and (3) determining the statistical significance of the measure. The gravimetric proportion of the diet contributed by prey category j(p_j) can be estimated as the total weight of prey category j in all stomach samples divided by the total weight of all prey categories combined (Hyslop 1980). Algebraically this is expressed as

$$p_j = \frac{\sum_k w_{jk}}{\sum_j \sum_k w_{jk}} = \frac{w_{j.}}{w_{..}} \qquad (1)$$

where w_{jk} is the weight of prey category j for individual k, $w_{j.}$ is the total weight of prey category j summed across all individuals, and $w_{..}$ is the total weight of all prey. Each p_j is transformed to x_j, where $x_j = \arcsin \sqrt{p_j}$, so that it conforms more closely to a normal random variable (Sokol and Rohlf 1969). Because x_j is estimated as a pooled proportion rather than the average of the proportions for individual fish, the variance of x_j and the covariance between x_j and x_i cannot be calculated directly and instead are approximated by using the delta method (Seber 1973). In the following, $\mathbf{x}_i$ indicates the vector of x_j for sample i, and $\mathbf{S}_i$ indicates the matrix of variance and covariance estimates for $\mathbf{x}_i$.

The measure of statistical difference used is the Hotelling's T^2 statistic, a multivariate extension of the t-statistic (Morrison 1976). In matrix notation, this statistic is expressed as

$$T^2 = (\mathbf{x}_1 - \mathbf{x}_2)' \, \mathbf{S}_{\cdot}^{-1} \, (\mathbf{x}_1 - \mathbf{x}_2), \qquad (2)$$

where $\mathbf{S}_{\cdot}^{-1}$ is the inverse of the pooled estimate of the variance-covariance matrix (Morrison 1976). $\mathbf{S}_{\cdot}$ is approximated, assuming reasonably large sample sizes (>50 stomachs with prey per sample), as

$$\mathbf{S}_{\cdot} = \frac{2(N_1 \mathbf{S}_1 + N_2 \mathbf{S}_2)}{N_1 + N_2}, \qquad (3)$$

where N_1 and N_2 are the sizes of the two samples.

Once a value of T^2 is computed, its significance is determined from an empirical probability distribution of T^2 computed by using a technique known as randomization (Edgington 1987). Computation of the empirical probability distribution using this technique proceeds as follows: (1) stomach content data from both time or area samples are

Manuscript accepted 12 October 1990.
Fishery Bulletin, U.S. 89:167–169 (1991).

Table 1
Probability levels associated with the randomization tests of the individual hypotheses. Because these are *a posteriori* tests, significance levels were adjusted according to the Bonferroni inequality to 0.25α ($^{*}P \leq 0.0125$, $^{**}P \leq 0.0025$).

	Mean proportion			
	Sample 1	Sample 2	t-value	Probability level
Tunicates	0.32	0.69	−9.1	<0.001**
Crustaceans	0.27	0.13	5.0	0.011*
Fish	0.26	0.10	3.7	0.046
"Others"	0.15	0.08	1.9	0.294

combined, (2) the combined data are randomly sorted into two new samples equal in size to the originals, and (3) a value of T^2 is calculated for the two samples. Steps 2 and 3 are repeated iteratively (the present study uses 5000 iterations), and the probability distribution of the randomized values of T^2 is then calculated. Next, the significance level of obtaining the original T^2 is estimated by determining the proportion of the randomized T^2 values that, ignoring signs, is equal to or greater than the original.

If between-sample equality of the diet is rejected, it is then appropriate to test for the equality of individual prey categories to determine which categories contribute most to the difference in diet. In this case, the measure of statistical difference used is the univariate t-statistic. In matrix notation, the vector of t-statistics (**t**) can be computed as

$$\mathbf{t} = \mathbf{D}.^{-1}(\mathbf{x}_1 - \mathbf{x}_2), \quad (4)$$

where $\mathbf{D}.^{-1}$ is the inverse of a matrix formed from the diagonal elements of $\mathbf{S}$.. As before, the significance of each t-statistic is determined from an empirical probability distribution computed for each prey category using randomization. Computation of these probability distributions is identical to that described for the multivariate case, except that a matrix of univariate t-statistics (Eq. 4) is used in the calculation instead of the T^2-statistic (Eq. 2). These individual tests are *a posteriori* tests and require some adjustment of the error rate considered to be significant. Using the Bonferroni inequality (Morrison 1976, Miller 1981), an appropriate adjustment is to assume significance at $\alpha \cdot n^{-1}$.

The above procedures have been incorporated into the computer program DIETTEST, which is designed to run on IBM-compatible microcomputers. This program is available from the author.

As an example of the application of this method, it has been used to test for dietary differences between two samples of pelagic armorhead: 55 fish collected in June 1985, and 101 fish collected in August 1988 (only fish with prey in their stomachs were used in the analysis). Both samples were obtained from the Southeast Hancock Seamount (lat. 30°N, long. 180°W) on the Hawaiian Ridge. Stomach contents were sorted to the lowest taxonomic category possible, then blotted and weighed to the nearest milligram. To simplify the analysis, various prey items were pooled into four major prey categories: tunicates, crustaceans, fish, and "others."

Results and discussion

When the method was applied to the two armorhead samples, the test of the simultaneous equality of all dietary proportions between samples was highly significant ($P<0.001$), indicating that the diet of pelagic armorhead had changed between the two sampling periods. Because of this, tests were also made for individual prey categories. Two of the four prey categories, tunicates and crustaceans, differed significantly between samples (Table 1) and therefore appeared to be responsible for the overall difference in diet.

The measure of between-sample difference, T^2, employed in the proposed test was selected primarily because the absolute differences between samples are scaled by the within-sample variances, a particularly desirable feature when dealing with highly variable quantities such as fish diets. This choice, however, imposes a constraint on the proposed statistical test; that is, the method can only be applied to cases in which the two diet samples lack mutually exclusive components. This constraint arises because computation of T^2 requires inversion of the variance-covariance matrix (Eq. 2) which is singular and therefore not invertible when a prey category is completely absent from one of the samples. Although this constraint may not be severe when the diet of a single predator is being examined for spatial or temporal variation, especially if one is willing to accept the pooling of prey to relatively high taxa, the proposed method is likely to be of limited value for comparing the diets of different predators. For such between-predator comparisons, a more appropriate test could be developed by utilizing some measure of diet overlap (Caillet and Barry 1979) which is not affected by mutually exclusive prey categories, instead of T^2 as a measure of between-sample difference.

Acknowledgments

I thank George Boehlert, Tim Gerrodette, John Hoenig, Russell Kappenman, Jeff Polovina, and two anonymous

referees for reviewing the manuscript and offering helpful suggestions. In addition, I thank Donald Kobayashi for his programming assistance and Mike Seki for initially posing the problem.

Citations

Caillet, G.M., and J.P. Barry
1979 Comparison of food array overlap measures useful in fish feeding habit analysis. *In* Lipovsky, S.J., and C.A. Simenstad (eds.), Gutshop '78 fish food habits studies; Proceedings of the second Pacific Northwest technical workshop, October 10–13, 1978, Maple Valley, Washington, p. 67–79. Wash. Sea Grant Publ., Univ. Wash., Seattle.

Crow, M.E.
1979 Multivariate statistical analysis of stomach contents. *In* Lipovsky, S.J., and C.A. Simenstad (eds.), Gutshop '78 fish food habits studies; Proceedings of the second Pacific Northwest technical workshop, October 10–13, 1978, Maple Valley, Washington, p. 87–96. Wash. Sea Grant Publ., Univ. Wash., Seattle.

Edgington, E.S.
1987 Randomization tests, 2d ed. Marcel Dekker, NY, 341 p.

Ellison, J.P.
1979 The use of discriminate analysis in the study of fish food habits. *In* Lipovsky, S.J., and C.A. Simenstad (eds.), Gutshop '78 fish food habits studies; Proceedings of the second Pacific Northwest technical workshop, October 10–13, 1978, Maple Valley, Washington, p. 80–86. Wash. Sea Grant Publ., Univ. Wash., Seattle.

Hyslop, E.J.
1980 Stomach contents analysis—a review of methods and their application. J. Fish. Biol. 17:411–429.

Miller, R.G. Jr.
1981 Simultaneous statistical inference, 2d ed. Springer-Verlag, NY, 299 p.

Morrison, D.F.
1976 Multivariate statistical methods, 2d ed. McGraw-Hill, NY, 415 p.

Pinkas, L., M.S. Oliphant, and I.L.K. Iverson
1971 Food habits of albacore, bluefin tuna, and bonito in California water. Calif. Dep. Fish Game. Fish. Bull. 152, 105 p.

Seber, G.A.F.
1973 The estimation of animal abundance and related parameters. Hafner Press, NY, 506 p.

Sokol, R.R., and F.J. Rohlf
1969 Biometry. W.H. Freeman, San Francisco, 776 p.

The National Marine Fisheries Service (NMFS) does not approve, recommend, or endorse any proprietary product or proprietary material mentioned in this publication. No references shall be made to NMFS, or to this publication furnished by NMFS, in any advertising or sales promotion which would indicate or imply that NMFS approves, recommends or endorses any proprietary product or proprietary material mentioned herein, or which has as its purpose an intent to cause directly or indirectly the advertised product to be used or purchased because of this NMFS publication.

Fishery Bulletin

Guidelines for Contributors

Form of manuscript

The document should be in the following sequence: Title Page, Abstract (not required for Note), Text, Acknowledgments, Citations, Text footnotes, Appendices, Tables, Figure legends, and Figures.

Title page should include authors' full names and mailing addresses and the senior author's telephone and FAX numbers.

Abstract Not to exceed one double-spaced typed page. Should include a sentence or two explaining to the general reader why the research was undertaken and why the results should be viewed as important. Abstract should convey the main point of the paper and outline the results or conclusions. No footnotes or references.

Text A brief introduction should portray the broad significance of the paper. The entire text should be intelligible to readers from different disciplines. All technical terms should be defined, as well as all abbreviations, acronyms, and symbols in text, equations, or formulae. Abbreviate units of measure only when used with numerals or in tables and figures to conserve space. Measurements should be expressed in metric units, with other equivalent units given in parentheses. Follow the *U.S. Government Printing Office Style Manual*, 1984 ed., and the *CBE Style Manual*, 5th ed. Fishery and invertebrate nomenclature should follow the *American Fisheries Society Special Publication 12* (for fishes), *16* (for mollusks), and *17* (for decapod crustaceans).

Text footnotes should be numbered in Arabic numerals and typed on a separate sheet from the text. Footnotes are not used for reference material or personal communications, but rather to explain or define terms in the text and for contribution numbers on the title page.

Informal sources Personal communications, unpublished data, and untitled manuscripts in preparation are noted parenthetically in the text (full name, affiliation, brief address including zip code, and month and year when appropriate).

Acknowledgments Gather all acknowledgments into a brief statement at the end of the text. Give credit only for exceptional contributions and not to those whose contributions are part of their normal duties.

Citations All titled sources should be listed in the Citations section, including unpublished and processed material. In text, cite as Smith and Jones (1977) or (Smith and Jones 1977); if more than one citation, list chronologically (Smith 1936, Jones 1975, Doe In press). All sources cited in the text should be listed alphabetically by the senior authors' surnames under the heading CITATIONS. Abbreviations of periodicals and serials should conform to *Serial Sources for the BIOSIS Data Base*™. Indicate whether sources are in a language other than English. For informal literature, include address of author or publisher. Authors are responsible for the accuracy of all citations.

Tables should supplement, not duplicate, the text. Each table should be numbered and cited consecutively, with headings short but amply descriptive so that the reader need not refer to the text. For values less than one, zeros should precede all decimal points. Indicate units of measure in column headings; do not deviate from the unit of measure within a column. Table footnotes should be noted consecutively in Roman letters across the page from left to right and then down. Since all tables are typeset, they need not be submitted camera-ready.

Figures Photographs and line drawings should be of professional quality—clear and concise—and reducible to 42 picas for full-page width or to 20 picas for a single-column width, and to a maximum 55 picas high. All graphic elements in illustrations must be proportioned to insure legibility when reduced to fit the page format. Line weight and lettering should be sharp and even. Lettering should be upper and lower case, and vertical lettering should be avoided whenever possible (except for vertical, y, axis). Zeros should precede all decimal points for values less than one. Reproductions of line artwork are accepted in the form of high-quality photographic prints from negatives or photomechanical transfer (PMT). Halftones should be sharply focused with good contrast. Micron rules should be inserted on electron micrographs, even when magnification is included in the figure legend. There should be clear distinction between identifying letters (press-on or overlay) and background of photograph. Label each figure in pencil on the back. Send only xerox copies of figures to the Scientific Editor; originals or photographic prints will be requested later when the manuscript is accepted for publication.

Copyright Government publications are in the public domain, i.e., they are not protected by copyright.

Submission of manuscript

Disks Authors are encouraged to retain manuscripts on word-processing storage media (diskettes, floppy disks) and submit a double-spaced hardcopy run from the storage media. Submit disks as MS-DOS "print" or "nondocument" files (often called "ASCII files"). If a disk cannot be converted to an ASCII file, the author should indicate on the disk the source computer and software language along with the file name. Either 5¼-inch or 3½-inch disks from IBM-compatible or Apple/MacIntosh systems (non-graphics only) can be submitted, double-sided/double-density or high-density, limiting each file to 300 kilobytes. All 8-inch word-processing disks (e.g., Wang or NBI) must be converted onto 5¼- or 3½-inch MS-DOS print disks.

Send original hardcopy and two duplicated copies to:

Dr. Linda L. Jones, Scientific Editor
National Marine Mammal Laboratory F/AKC3
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE
Seattle, WA 98115-0070

Copies of published articles and notes The senior author and his/her organization each receive 50 separates free-of-charge. Additional copies may be purchased in lots of 100.